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Functional Attributes of Post-Disturbance Regeneration in Puerto Rican Tropical Dry Forest

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FUNCTIONAL ATTRIBUTES OF POST-DISTURBANCE REGENERATION IN PUERTO RICAN TROPICAL DRY FOREST

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ABSTRACT

The global extent of tropical dry forests has rapidly diminished in recent decades due to a variety of threats, largely from human activity. Efforts to restore these forests require understanding of the various modes of regeneration and how they are impacted across a range of disturbance-types. Studies of tropical forest recovery have traditionally neglected the concept of 'persistence' in favor of 'recruitment' and seedling dynamics. Increasingly, the role of resprouting as a form of persistence in stressful environments is recognized as an important factor that has implications for population turnover, minimizing disturbance impacts and reducing reliance on seeds. Using a functional-trait approach, this research investigated the functional basis of resprouting and persistence within tropical dry forest from the individual to community scale. The study area was a threatened Puerto Rican tropical dry forest where resprouting is a dominant form of recovery and thought to be an adaptation to drought and occasional windthrow. Firstly, I sought to determine the range of functional types within the community by asking what water-use strategies characterize dominant tree species? A broad range of water-use behaviors were observed but most species converged on a high degree of drought tolerance maintaining dry season resource uptake. Secondly, I considered the life-history consequences associated with resprouting. Conservative, drought tolerant strategies were associated with low adult growth, which unexpectedly also translated to weaker resprouting. The occurrence of Hurricane Maria presented the opportunity to study the short-term physiological responses of trees following defoliation. Interestingly, dry forest species were found to exhibit highly plastic responses suggesting a common ability to exploit high resource windows possibly to fuel recovery. Finally, I asked whether functional recovery and assembly mechanisms were predictable across clearcut and fire chronosequences where resprouting was the dominant form of regeneration. Both types of chronosequences were characterized by functional shifts from conservative to more acquisitive

resource-use, but recovery trajectories in clearcut sites were more stable as the effects of lower disturbance severity promoted successful regeneration of resprouts similar to ‘natural’ patterns of recovery. Fire legacy effects by contrast inhibit functional diversity and create species poor communities. Overall, my results suggest that successful persistence through resprouting in tropical dry forest is strongly dependent on species identity, life-history strategy and the type of disturbance. These forests have a diversity of mechanisms available to drive recovery but severe disturbances such as fire will reduce that diversity and ultimately reduce forest resilience.

DEDICATION

This work is dedicated to my wonderful grandparents Janine Y.G. Ribeiro, Barbara A. Allerton, Pierre O. Lorléac’h and Peter G. Allerton.

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CHAPTER ONE

INTRODUCTION

It is estimated that tropical and subtropical dry forest accounts for 42% of the total global tropical forest cover (Murphy & Lugo, 1986a). Historically, tropical dry forests (TDF) have been exposed to significant degradation from human activities including clearing for agricultural, cutting of valuable trees, as sources for fuel wood and exposure to wildfires, threats that continue to a large extent today (Gerhardt & Hytteborn 1992; Murphy & Lugo 1986a; Miles *et al*., 2006). Restoration is hindered in part, because there is a lack of knowledge regarding the specific regeneration attributes of TDFs (McDonald *et al.*, 2010; Vieira & Scariot, 2006). Unlike in tropical wet environments, regeneration in TDF is not facilitated by the opening of gaps in the canopy; and moisture availability is known to be a critical determinant of successful seedling establishment. Rather, regeneration in many TDFs after disturbance is driven primarily by vegetative reproduction (i.e. resprouting), in particular when disturbance intensities do not result in the total loss of above-ground biomass (Ewel, 1977; Murphy *et al.*, 1995; Van Bloem *et al.*, 2003; Allerton, 2013).

General successional theory has provided us with a good understanding of species compositional turnover within disturbed sites over time. However, still unclear are the specific functional roles species play within a community during recovery, or how establishment of species with particular functional traits may facilitate later establishment of new species; information that is important to creating effective restoration pathways. Surprisingly, considering the continued over-exploitation of TDFs, relatively few studies

are conducted regarding their ecology and regeneration thus inhibiting efforts to restore these forests (Viera & Scariot, 2006). *As plant persistence and recovery within many TDFs is dependent on resprouting, my dissertation will focus particularly on the underlying functional mechanisms that characterize resprouting response from the individual to the community level in an endangered Caribbean TDF ecosystem. To achieve this, my research adopts a functional trait-based approach to determining genetic attributes of TDF species that serve to maximize their chances of survival and that can be employed in conservation efforts going forward (Ostertag et al., 2015).*

The structure of this dissertation begins with a summary of the characteristics that define tropical dry forests generally and specifically in Puerto Rico. Chapter 2 will cover a brief review of the role of resprouting as a mechanism of persistence and recovery in disturbed ecosystems including gaps in our knowledge. The review will end with the overarching research objectives for this dissertation including a conceptual representation of how objectives are linked to enhancing our understanding of resprouting and persistence in TDF systems. The four research objectives are covered in Chapters 3-6 and finally I finish with some concluding thoughts as well as implications of my research and future research questions.

STUDY SYSTEM – TROPICAL DRY FOREST

Moist forests and savannas are iconic tropical biomes that attract significant research attention. Far less attention, however, is paid towards tropical dry forests (TDFs) despite their widespread global distribution and provision of critical habitat and important

ecosystem services. According to the Holdridge life zone classification system, TDFs occur in regions exempt from frost, where mean annual temperatures >17$_{o}$C, mean annual precipitation is 500-2000mm and potential evapotranspiration exceeds precipitation. Dry forests are known for their pronounced dry seasons (<50mm rainfall) which can last 3-10 months per year. Perhaps as important however, is the significant variation that exists between forests in both the distribution of rainfall throughout the year and the overall total amount. The seasonal drought stress to flora and fauna that accompanies such precipitation dynamics separate TDFs from tropical moist forests and the lack of a natural fire regime differentiates them from savannas. As such, TDFs have distinct ecosystem function justifying their categorization as a unique biome.

Although biodiversity is comparably lower than that found in tropical moist forests, TDFs contain proportionately more locally and regionally endemic species further highlighting their conservation value. However, these ecosystems are severely under threat due to their fertile soils and distribution in favorable climates often placing them in direct conflict with the agricultural, development and logging needs of humans. Some reports even suspect the threat to dry forests from deforestation exceeds that in tropical moist forests (Aldhous, 1993; Blackie *et al.*, 2014). In the Neotropics, the effect of land-use change on TDFs is evident based on Janzen's (1988) assessment that less than 2% of original dry forests still persist in their natural form. The effects of climate change have introduced new uncertainties around how altered rainfall regimes might influence the survival of trees, many of which are considered to be already living close to their physiological limits (Choat *et al.*, 2012). Most of these threats are likely to accelerate as

human population densities increase and therefore TDFs are a prime candidate for investment towards their conservation and restoration.

TROPICAL DRY FOREST IN PUERTO RICO

The vast majority of Puerto Rico's tropical dry forest occurs along the southwestern coast of the island of Puerto Rico between Cabo Rojo in the west and Guayama in the east (Fig. 1.1). Although TDFs only comprise 15.5% of the total forest area in Puerto Rico, they are the only forest type to occur on all five of Puerto Rico's islands (Miller & Lugo, 2009). On the island of Puerto Rico itself, the dry forest zone occurs in the orographic rain shadow of the Cordillera Central mountain system (Murphy *et al.*, 1995). Here, mean annual precipitation ranges from 600-1000 mm with considerable interannual variability (Lugo *et al.*, 1978). A pronounced dry season lasts from December to April with a shorter, more variable dry period during the summer months between June-August. However, there is typically a soil water deficit for approximately 10 months of the year and evaporative demand is greater than precipitation for at least 9 months of the year (Murphy *et al.*, 1995). Additional to drought periods, hurricanes are considered part of the disturbance regime in the region and have likely played a role in shaping the structure of Caribbean forests (Lugo *et al.*, 1981; Van Bloem *et al.*, 2005).

The majority of Puerto Rican TDF sits on a limestone formation dating back to around the Miocene-Oligocene Epoch. Soils are generally shallow, high in organic matter and possess relatively high nutrient status (Lugo & Murphy, 1986). However, the high soil pH is thought to cause P to bind with calcium and decrease overall bioavailability to

plants thus suggesting local plants may be P-limited (Van Bloem *et al.*, 2003). Topography is hilly, and elevations range from sea level by the coast to 228m (Murphy *et al.*, 1995). The large majority of the forest is made up of three vegetation associations that vary with elevation, slope, soil-depth, and moisture-holding capacity (Murphy *et al.*, 1995). Scrub forests dominate in shallow, sandy areas along the coastline. Further inland, short, dense semi-deciduous upland regions (Fig. 1.2) are interspersed with small valleys containing deeper alluvial and colluvial soils with taller semievergreen vegetation.

Overall, the area has a complex disturbance history that has included crop cultivation for maize, tobacco and sugar cane, as well as timber and charcoal production, grazing and housing development. Since abandonment, introduced N-fixing species including *Leucaena leucocephala* and *Prosopis juliflora* have played an influential role in forest succession. Human-caused wildfires occasionally occur on the forest peripheries, typically close to roads where they gradually encroach into native forest. Fire remains a consistent threat, in part due to the replacement of burnt native vegetation with invasive African grasses. These non-native grasses tend to act as excellent fuels during the dry season (Thaxton *et al.*, 2012) and promote recurring fires through the grass-fire cycle (D'Antonio & Vitousek, 1992). There are no known records of natural fires occurring in Guánica Forest (Murphy *et al.*, 1995).

The Caribbean TDF region has been determined as a distinctive phytogeographic region within the Neotropics, with a high level of species endemism (Dryflor, 2016). Additionally, in a phylogenetic analysis of the island-wide species pool across 15 protected forests, Guánica Forest exhibited the highest degree of tree-wide phylogenetic

clustering, which the authors interpreted as a sign that only a small cohort of lineages possess the ability to persist in the region due to the constrains imposed by harsh environmental conditions (Muscarella *et al.*, 2014). In short, Puerto Rican TDF represents a unique and biodiverse system that merits further study to understand how best to ensure its long-term preservation.

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FIGURES

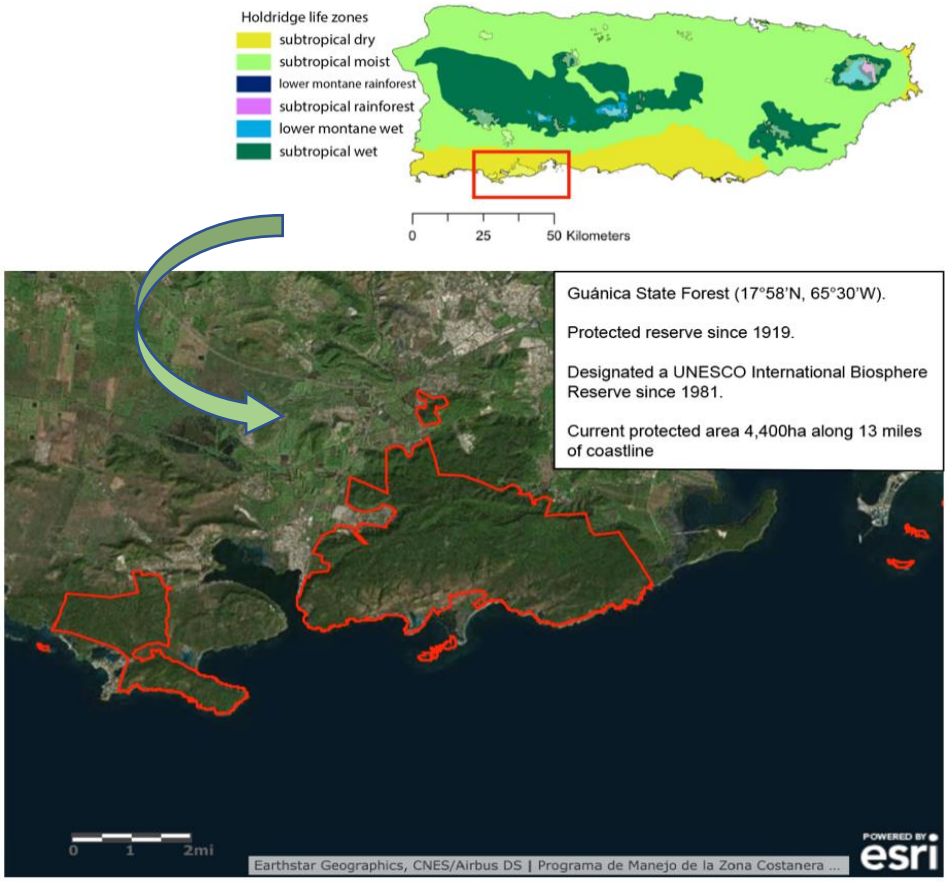

Figure 1.1. Delineated boundaries of Guánica State Forest (main image) and the distribution of ecological life zones on the island of Puerto Rico (above). Ecological life zone map adapted from Miller & Lugo (2009).

Figure 1.2. Semi-deciduous upland vegetation in Guánica dry forest, looking south along the Ballena trail. Note the relatively short, dense stature of the native forest vegetation.

CHAPTER TWO

RESPROUTING AS A KEY MECHANISM OF PERSISTENCE AND RECOVERY IN DISTURBED ENVIRONMENTS - A REVIEW

The ecology of resprouting is increasingly recognized as a cornerstone to the 'persistence niche' within many terrestrial plant environments, and as such has become an active field of research. The aim of this chapter is to briefly review the role of resprouting within the context of tropical dry forest regeneration together with the broader abiotic and biotic factors that govern resprouting within disturbed environments. The implications of resprouting for forest succession and community assembly are also discussed. Presentation of the overarching research objectives will follow that are designed around a resprouting conceptual model framework identifying the links between factors of interest that may influence resprouting responses and consequences of resprouting in Puerto Rican TDF systems.

THE COMPLEX DYNAMICS OF TROPICAL DRY FOREST RECOVERY

Mechanisms of regeneration among tropical forests vary greatly and are determined in large part by the dynamic interaction between resource availability and disturbance at the local scale. As a result, the ecological processes that determine successful regeneration can be complex as is demonstrated within tropical dry forests (TDF). While gap dynamics and changes in light availability are key to regeneration in tropical moist forests, they are not thought to be influential in TDF recovery where plant structural characteristics are considerably different (e.g. higher density, smaller trees, reduced

stratification) (Ceccon *et al.*, 2006; Dirzo *et al.*, 2011). More relevant are dramatic changes in water availability that are tied to seasonal rainfall patterns. For many species, optimal rates of seedling dispersal, germination, survival and growth synchronize with favorable rainy periods (Bullock *et al*., 1986; Khurana & Singh, 2000; McLaren & McDonald, 2003a). And yet, in the community as a whole there remains significant temporal variation in the phenological niches of co-occurring species, and together with the influence of biotic factors (e.g. frugivores) suggest reproduction dynamics in TDF are anything but straightforward (Lasky *et al*., 2016). Overall, seedlings are highly susceptible to the harsh conditions that occur within TDF environments, with significant evidence linking seedling mortality to low water availability (Slot & Poorter, 1997), soil nutrient limitation (Murphy & Lugo, 1986), changes in canopy cover and light availability (Gerhardt, 1996a; Poorter *et al.*, 2009) and herbivory (Gerhardt, 1998; Howlett & Davidson, 2003). Thus, numerous factors must confluence to ensure successful recruitment of seedlings in TDF.

Vegetative reproduction is an alternative recovery mechanism that is widespread throughout the tropics, but its relative importance within forests is thought to vary inversely with local productivity (Bellingham & Sparrow, 2000; Lamont *et al.*, 2011; Clarke *et al.*, 2013). As an illustration, although wet and dry forests appear to have comparable potential to resprout, the ratio of resprouts to seedlings is considered much higher in dry forests (Ewel, 1977). Hence, resprouting may have an important role enhancing TDF resilience where seedling success rates are low (McLaren & McDonald, 2003b; Viera & Scariot, 2006; McDonald *et al.*, 2010). At the same time, TDFs vary

greatly in their precipitation regimes resulting in noticeable differences among sites in the relative contribution of seed establishment vs resprouting (Khurana & Singh, 2000; Allen *et al.* 2017) and even within particular sites, resprouting and seedling establishment are known to vary between years, species and different disturbance types (Allen *et al.* 2017). The intensity and frequency of natural disturbances in Neotropical TDF (primarily drought and wind) are considered strong selective forces in the promotion of resprouting, in part because natural disturbances tend not to result in the total loss of above-ground biomass therefore leaving available buds and resources to fund regrowth (Ewel, 1977; Murphy & Lugo, 1986; Murphy *et al.*, 1995; McLaren & McDonald, 2003c). Ultimately, resprouting has beneficial effects at both the community and individual level in the form of both shorter recovery times of lost biomass as well as enabling previously dying trees to 'resurrect' from residual buds (Ewel, 1980).

THE DIFFICULTIES OF DEFINING RESPROUTING AS A FUNCTIONAL TRAIT

Plant species throughout the terrestrial world are capable of initiating vegetative reproduction through dormant meristematic tissues in response to a change in environmental conditions or the loss of biomass from disturbance. Within research circles, both 'sprouting' and 'resprouting' have been used interchangeably to describe this process of recovery (see Bellingham & Sparrow, 2000; Bond & Midgley, 2001; Del Tredici, 2001) however, Clarke *et al.* (2013) has called for greater consistency among researchers. Specifically, the authors argue 'sprouting' is a general term that describes the initiation of growth from buds without necessarily the involvement of disturbance,

whereas disturbance is explicitly embedded in the term ‘resprouting’ as it encompasses the act of repeated vegetative regeneration from bud and meristematic sources. Accordingly, this study will explicitly use the term ‘resprouting’ in all further references to recovery via vegetative regrowth following disturbance.

Resprouting has proved a difficult trait to measure and compare among disparate sites. Studies from fire-prone systems tend to characterize interspecific resprouting ability using binary classifications (e.g. R+ vs R-), a method admittedly that has proved somewhat effective in discerning functional and life-history differences between resprouters and non-sprouters (Bell & Ojeda, 1999; Lamont & Wiens, 2003; Knox & Clarke, 2005; Vilagrosa *et al.*, 2013). However, this method may lead to the loss of large amounts of biological information, especially where disturbances are less intense and regrowth responses are more diverse (Vesk & Westoby, 2004; Poorter *et al.*, 2010). On account of this, there is a need to more precisely quantify resprouting properties in order to capture the continuum of responses that plants have been found to exhibit. Ontogenetic shifts in resprouting ability must also be considered in any study of resprouting. The precise reasoning for such shifts is unclear but may be connected to physiological, anatomical and genetic changes through time (Del Tredici, 2001). A meta-analysis by Vesk (2006) across a range of terrestrial biomes found evidence that the relationship between resprouting and ontogeny changes between growth forms. Specifically, ground-dwellers were capable of resprouting regardless of age, whereas resprouting increased with age in shrubs but decreased in trees. Interestingly, the authors determined differences in bud longevity among growth forms were likely responsible as well as

adaptive responses linked to the inability of juveniles to avoid fire. For the purposes of this dissertation, focus is placed on resprouting among adult tree individuals as this specifically relates to the concept of persistence whereas resprouting among saplings is more closely aligned to the 'regeneration niche' (Grubb, 1977).

DROUGHT OCCURS ACROSS THE TROPICS, BUT ITS LINK TO RESPROUTING IS UNCLEAR

In tropical latitudes, water availability is perhaps the single most important resource governing ecosystem structure, composition and functioning (Vitousek et al. 1997, Markesteijn, 2011; Bonal *et al.*, 2016; Corlett, 2016). Tropical regions are characterized by high solar radiation, high evapotranspiration and strong precipitation seasonality which is strongly linked to latitudinal fluctuations in the inter-tropical convergence zone (Bonal *et al.*, 2016). Both annual rainfall and rainy season length have considerable spatial variation but generally decrease with increasing distance away from the equator. Together with the significant interannual variability that can occur (e.g. El Nino), a broad range of rainfall patterns exist which are poorly captured within commonly used terminology of tropical systems and weather regimes (e.g. 'wet' or 'dry' forest/ season). TDFs and savannas capture this variation well by possessing seasonal rainfall distributions that themselves can vary dramatically in length and intensity as well as among years and sites (Allen *et al.*, 2017). Tropical moist/ wet forests also experience their own dry periods characterized by rainless intervals within wet seasons or drought periods that tend to occur in cycle with El Niño Southern Oscillations. Importantly,

variations in water availability translate to changes regarding the distribution and diversity of tropical forest species across multiple scales: from regional-scale differences associated with broad rainfall gradients (Swaine, 1996; Joseph *et al.*, 2012) to more locally driven vegetation changes that are determined by topographical gradients in moisture (Gentry, 1998; Poorter *et al.*, 2010). To what extend these gradients are reflected in the distribution of functional and regeneration strategies within tropical plant communities however remains an open question. There is some indirect evidence that resprouters are more abundant where seasonal drought and higher interannual variability in precipitation occur. Keeley (2014) demonstrated that among trees and shrubs across 4000 sites in Australia exposed to both fire and regular seasonal drought that the overall abundance of resprouters tends to increase with increasing interannual variability. Although there are no similar examples from TDF systems, studies describing tropical forest regeneration dynamics have found resprouting is somewhat widespread in areas associated with variable rainfall regimes (Murphy & Lugo, 1986b) as well as where drought and wind stress interact (Van Bloem *et al.*, 2003; Jimenez-Rodríguez *et al.*, 2018).

CHARACTERIZING THE DROUGHT RESPONSES OF RESPROUTERS

Divergence in traits, biomass allocation and water relations indicate alternative drought responses between resprouting and non-sprouting species (Zeppel *et al.*, 2015). However, studies from different systems have reported conflicting findings into how species with alternative regeneration life-histories use water. As an illustration, where fire-regimes

dominate such as in Mediterranean-type environments, measurements of resprouters have shown lower rates of gas-exchange and xylem-specific conductance but higher cavitation resistance, lower vessel density and larger vessel diameter than coexisting non-sprouters (Vilagrosa *et al.*, 2014). Post-fire resprouters also show higher leaf mass per area (LMA), leaf dry matter content and area-based leaf nitrogen (Schwilk & Ackerly, 2005; Paula & Pausas, 2006). In effect, this suite of traits characterizes resprouters as 'conservative' resource users relative to non-sprouters with overall greater drought tolerance aided by sclerophyllous leaves or deeper roots. Interestingly however, initial observations from hurricane-prone tropical environments have suggested resprouters may possess acquisitive water-hungry resource strategies (Paz *et al.*, 2018; Jimenez-Rodríguez *et al.*, 2018) in what appears to be in direct contrast to findings from Mediterranean systems. Thus far however, evidence from tropical areas has been restricted to just a handful of traits limiting our ability to accurately position resprouting species across axes of resource-use. Such information will aid in efforts to develop broad-scale predictions of productivity patterns under a changing climate as well as describe the distribution of species across spatial and temporal scales of moisture availability.

Higher biomass allocation patterns among resprouters vs nonsprouters may confer a fitness advantage during periods of drought. In order to optimize performance in stressful environments, plants appear to invest a greater proportion of resources to structures designed to capture limiting resources (i.e. in this case water, but also light and nutrients in other environments), as posited by Bloom *et al.*'s (1985) optimal partitioning theory. This is well demonstrated by the high root:shoot ratios found in many dry

environments enabling plants to better seek out water during drought (Poorter *et al.*, 2012; Qi *et al.*, 2019). In TDF systems where resprouting is a common trait, trees dedicate a far greater proportion of biomass to roots (up to 50%) relative to wet forests (Murphy & Lugo, 1986a). Furthermore, the concentration of root non-structural carbohydrates (NSC) has been found to be higher in resprouters relative to nonsprouters among woody shrubs in Australia (Knox & Clarke, 2005) as well as higher at the whole-plant level among a diverse set of dicotyledonous species within the same region (Pate *et al.*, 1990). Under favorable conditions, rates of overall growth among resprouters vs nonsprouters will be lower (Bellingham & Sparrow, 2000; Bond & Midgely, 2001; Vest & Westoby, 2004). However, under drought conditions resprouters have been shown to maintain higher relative growth rates relative to nonsprouters in Mediterranean shrublands (Ramirez *et al.*, 2012). Interestingly, one study found similar growth rates among congener resprouting and nonsprouting shrub seedlings with the authors concluding resprouters may be capable of leaf-level adjustments in photosynthesis in order to meet additional demands for storage (Knox & Clarke, 2005). Among resprouters only, where species position along a continuum of resprouting vigor (i.e. the rate of vertical growth) is also thought to be tied to the quantity of storage reserves, together with the intrinsic growth rate of species (Gurvich *et al.*, 2005). Although a higher rate of growth may imply greater resprouting vigor, according to the well-established trade-off between allocation to storage vs growth, fast-growing species are also expected to have weaker resprouting syndromes as they dedicate fewer assimilates to reserves to fund resprouting. Overall, differences in the functional strategies of coexisting resprouter and

nonsprouter species indicate a greater tolerance to drought among resprouters that may result in lower levels of drought-induced mortality due to the effects of climate change. This is supported by field experiments, where resprouters performed significantly better in their rates of survival and post-disturbance growth under a range of drought intensities (Pratt *et al.*, 2012, West *et al.*, 2012).

Alternatively, drought-related effects on resprout growth have been shown to have positive consequences for above-ground productivity. Temperate zones have reported higher rates of root suckering following extended periods of drought as higher soil temperatures aid in auxin degradation in the roots, thus promoting root growth and cytokinin synthesis which can stimulate root sucker initiation (Frey *et al.*, 2003). Such processes may explain the high rate of multi-stemmed individuals in Neotropical TDF as strong seasonal droughts may induce a resprouting response (e.g. Dunphy *et al.*, 2000).

THE IMPORTANCE OF STEM PERSISTENCE FOLLOWING DISTURBANCE TO RECOVERY

The expression of the resprouting trait is determined by the severity, frequency and variability of disturbance rather than the mechanism of damage itself (e.g. fire vs drought) because these aspects of disturbance impact on the availability and protection of buds and the necessary resources to fund regrowth (Vesk & Westoby 2004; Enright *et al.*, 2011; Clarke *et al.*, 2013; Zeppel *et al.*, 2015). Disturbance regimes that occur relatively frequently and have severe impacts for instance in certain fire-prone systems (e.g. dry Mediterranean heathlands, Ojeda *et al.*, 1996) will dramatically reduce above-ground

biomass and promote basal or underground resprouting, in contrast to lower severity fire systems (e.g. the Cerrado in Brazil, Miranda *et al.*, 2008) where stems and canopies often survive and axillary or epicormic sprouting drive recovery. When resprouting can occur from pre-existing stems there may be swift recovery of biomass and canopy cover as well as quicker restoration of biochemical nutrient cycling, hydrological cycles and habitat relative to sites subjected to higher disturbance intensities (Keeley *et al.*, 2014). Disturbance severity may also select specific spatial allocation patterns of NSCs. For instance, where there is total destruction of above-ground biomass plants are forced to remobilize below-ground NSC stores and therefore adapt to prioritize below-ground storage (Clarke *et al.*, 2013). Unsurprisingly, greater above-ground storage is more common where stems and canopies are not totally lost as observed in the wet tropics (Würth *et al.*, 2005) although there do appear to be examples where this is not always the case (Hoffmann *et al.*, 2003). Efforts to quantify NSC contents in temperate and tropical zones suggest NSC reserves among resprouters exceed those necessary to respond to a single disturbance event (Knox & Morrison 2005; Enright *et al.*, 2011; Paula & Ojeda, 2009) however, an increase in disturbance frequency may still serve to deplete NSC stores. For instance, there is indirect evidence shorter fire intervals disproportionately negatively affect basal and underground resprouters, presumably because epicormic resprouters rely on comparatively larger stem stores (Knox & Morrison, 2005).

Despite evidence that tree species likely draw upon NSC stores to fund resprouting post-disturbance (Hartmann & Trumbore, 2016), species may also seek to subsidize regrowth using new assimilates as quickly as possible and therefore minimize

depletion of NSC stores (Bond & Midgley, 2001). When high rates of above-ground biomass are lost, this process takes longer as regrowth of crown structures is essentially 'reset'. Preservation of stems after less intense disturbance however increases the opportunities for trees to enhance resource capture at the leaf level via plastic responses. So called 'compensatory responses' are a direct reference to the shifts in physiological and morphological traits plants have been observed to exhibit in order to enhance rates of assimilation in response to physical duress (McNaughton, 1983; Collin *et al.*, 2000). Plastic responses in leaves have been relatively well documented in experiments simulating herbivory (Lopushinsky & Klock, 1979; Reich *et al.*, 1993; Vanderklein & Reich, 1999; Blundell & Peart, 2001) where enhancements of resource uptake are often demonstrated or inferred to increase plant growth rate. In the context of tropical dry forest resilience and species persistence however, it is of interest whether trees may possess similar responses to hurricane disturbance, which is found could represent an important fuel source for recovery that has not previously been considered to any great degree.

RESPROUTING, TDF SUCCESSION AND COMMUNITY ASSEMBLY

Community assembly refers to the re-colonization processes responsible for shaping community structure, composition and the environment over the course of succession (Lebrija-Trejos *et al.*, 2010, Kraft & Ackerly, 2014). Study of community assembly theory can bring valuable insight towards methods of effective ecological restoration by revealing how species differ in their requirements for successful regeneration. Recent

studies have approached assembly as the result of two opposing extremes along a single niche axis: abiotic filtering whereby environmental conditions imposed on site select for stress tolerant and functionally similar species (Cornwell *et al.*, 2006) and competitive interactions (limited similarity, niche partitioning) that promote dissimilarity among coexisting species (MacArthur & Levins 1967; Chesson, 2000; Spasojevic & Suding, 2012). Community membership is initially dependent on possession of the appropriate traits to overcome dispersal filters as well as environmental stress (i.e. the abiotic filter) (Lebrija-Trejos *et al.*, 2010). Under this framework, when environmental stress is high then functional diversity among species is expected to be low but will rise over time with the gradual partitioning of resource niches (Weiher & Keddy, 1995).

The single niche axis theory however fails to take into account additional mechanisms that could be important to the assembly process (Mayfield & Levine, 2010). Where environmental stress is high, facilitative interactions between functionally distinct species can aid in the survival of individuals. For instance, habitat amelioration and increased shade from adult trees can facilitate growth and survival of seedlings and resprouts (Hastwell & Facelli, 2003; Santiago-Garcia *et al.*, 2008). Therefore, facilitation may promote dissimilarity among coexisting species and increase functional diversity within the community (Spasojevic & Suding, 2012). The role of increasing competitive hierarchies is considered influential and may demonstrate the competitive dominance of one species over others thus reducing trait variation and functional diversity (Mayfield & Levine, 2010). Alternatively, relatively weak competition and the partitioning of resources among species may be a sign that equalizing fitness processes are promoting

coexistence (Chesson, 2000). Stochasticity represents an additional process that could shift recovery away from general successional patterns (Hubbell, 2001). Ultimately, assembly can be complex and is dependent on a broad range of mechanisms capable of operating simultaneously at a given stage of succession (Spasojevic & Suding, 2012).

Studies of community assembly have traditionally focused on the role of seed dispersal, germination and seedling recruitment in the restructuring of plant communities however, there may be limited applicability of this approach in plant systems where resprouting is the dominant form of recovery. Caribbean dry forest communities dominated by resprouters are considered seedbank limited (Wolfe *et al.*, 2019), possibly linked to the trade-off in allocation to persistence vs reproduction (Clarke & Dorji, 2008; Clarke *et al.*, 2013). As a consequence, newly disturbed sites are limited in their seedling densities which may continue with succession depending on the extent of canopy closure and the relative impact of competition on resprouters (Clarke & Knox, 2009; Keeley *et al.*, 2012). Research from Australian shrublands have proposed recruitment rates may vary with fecundity favoring species that sprout vs seed (Enright *et al.*, 2007). Overall, the dominance of resprouters within regenerating communities may alter the mechanisms driving assembly compared to seedling dominated systems as competition is substituted for other processes (e.g. facilitation, niche differentiation) (Clarke & Knox, 2009).

RESEARCH OBJECTIVES AND CONCEPTUAL FRAMEWORK

The dissertation structure follows an adapted framework first put forward by Clarke *et al.* (2013) and is based upon gaps I have identified into possible influences on resprouting buds, their protection and resourcing mechanisms. This approach will allow for a better understand regarding the functional underpinning of resprouting among individuals and communities in Caribbean tropical dry forest (TDF). Caribbean TDF represents an endangered ecosystem with significant importance for biodiversity due to the high proportion of evolutionarily distinct species (Dryflor *et al.*, 2016). These forests have also received comparatively less attention relative to mainland TDFs (Blackie *et al.*, 2014). Tree resprouting is determined by the interaction between the abiotic environment that dictates growth and resource allocation, and the disturbance regime that diminishes buds and resources necessary to fund vegetative reproduction (Fig. 2.1). Tree physiology, mortality, and recruitment in Puerto Rican TDF is strongly dependent on the seasonal nature of precipitation which tends to be relatively low in quantity and highly variable in its distribution compared to other TDF sites (Allen *et al.*, 2017). During periods of drought stress, a trade-off occurs between maintenance of hydraulic integrity and carbon capture/photosynthesis (improving stores of non-structural carbohydrates) which in turn is regulated by physiological and morphological traits at the leaf, stem and root level (Plant functional traits: PFTs). Caribbean dry forest species have most likely evolved different strategies of water-use to regulate these trade-offs (Chapter 3) and their effects on tree performance and resprouting (Chapter 4). Phenotypic plasticity among key PFTs

may also be selected for to ‘assist’ regrowth dynamics in response to natural disturbances (Chapter 5). Overall, systematic differences in regeneration strategy among species or functional groups are likely to exist that can be identified through measurable traits that have been selected for by climate and historical disturbance regimes. Understanding how the functional trajectories of resprouting communities change over time following novel disturbances such as clearcutting and fire and the assembly mechanisms driving secondary succession (Chapter 6) will help us predict how tropical dry forest communities will respond to changing disturbance regimes linked to climate, land use change and new methods of conservation (e.g. alternative management systems). With that in mind, this dissertation seeks to gain insight into four specific questions:

- What water-use strategies characterize dominant tropical dry forest species in the Caribbean? (Chapter 3).
- What are the life-history consequences associated with resprouting in tropical dry forest? (Chapter 4).
- What are the short-term physiological responses that characterize TDF communities following a hurricane event? (Chapter 5).
- Are functional trajectories and mechanisms of community assembly predictable in a high resprouting TDF following ‘novel’ disturbance-types? (Chapter 6).

This dissertation primarily focuses on two important classes of resprouting – basal and below-ground. These two classes merit particular attention in this case because: 1) their

abundance within the resprouting literature allows for better comparisons between sites and systems; 2) the large amounts of historical data from the study area specific to these two classes of resprouting and; 3) their high relevance to recovery following both clearcutting and fire, two high intensity disturbance types of primary focus in this dissertation. Furthermore, only resprouting responses among adult individuals are included as they pertain directly to the concept of ‘persistence’.

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FIGURES

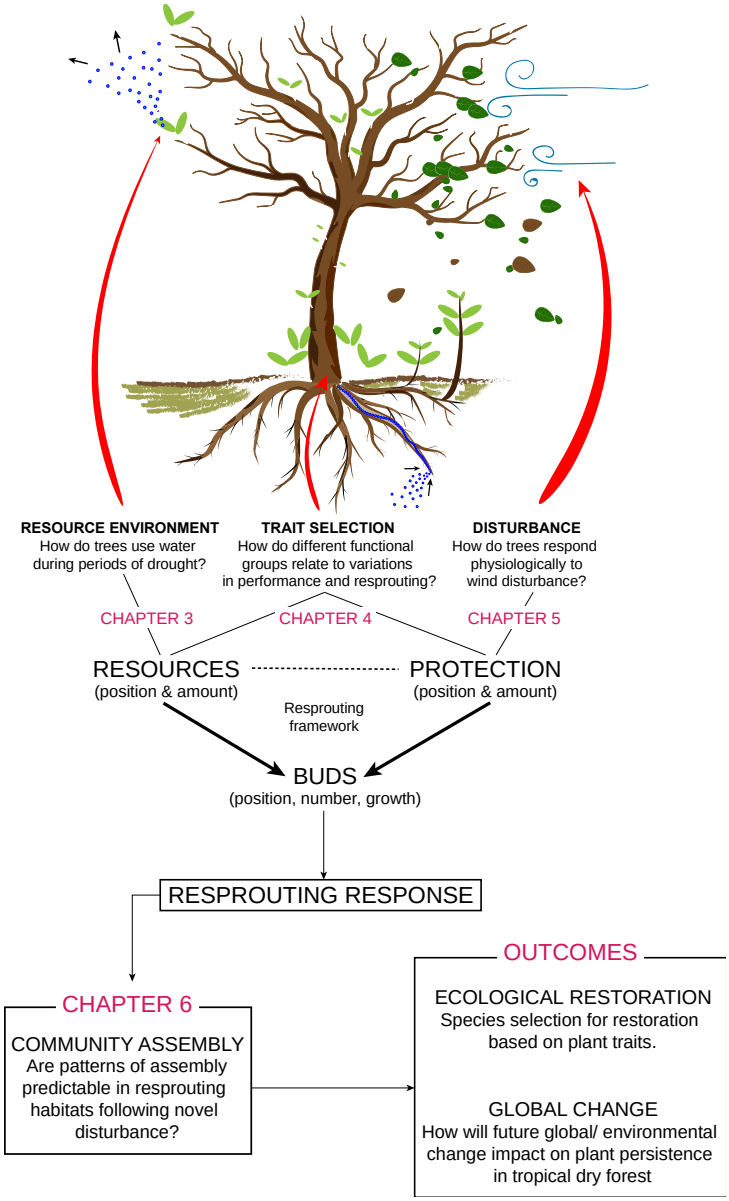

Figure 2.1. Conceptual framework outlining three axes of variation that drive resprouting from individuals to communities (buds, protection and resources). Thick black arrows indicate possible influences on resprouting. Thin arrows outline the consequences of variation in the resprouting framework. Modified from Clarke *et al.* (2013).

CHAPTER THREE

HYDRAULIC TRAIT VARIATION DEMONSTRATES MULTIPLE DROUGHT RESPONSE STRATEGIES AMONG LEAF HABITS IN MATURE CARIBBEAN DRY FOREST WITH LOW RAINFALL AND VARIABLE SEASONALITY.

ABSTRACT

1. Generalizing among tropical dry forests remains challenging due to their inherent ecological complexity. Functional shifts in plant water-use have been predicted to occur across climatic gradients which if true, could lead to a trait-based approach to classifying these systems. A wide range of water-use strategies have been documented in wetter, seasonally distinct regions however whether this extends to much drier, seasonally variable regions is uncertain.

2. We describe the water-use strategies and response to drought conditions of a taxonomically diverse group of 31 dominant tree species in Puerto Rico using a large set of physiological and morphological traits to determine: (i) if stressful environmental conditions due to low, inconsistent rainfall select for reduced trait variation within the tree community and; (ii) whether water-use is associated with leaf habit or growth form.

3. We found a large diversity of water-use adaptations among species with interspecific differences accounting for 67-94% of the total variation in traits. Although tree species fell along a continuum of strict isohydric to extreme anisohydric, a surprisingly large proportion exhibited maintenance or increases in gas-exchange under strong drought conditions. Such drought-tolerance was strongly tied to investment in wood density and leaf dry matter content. Relatively few species were considered strong drought avoiders (strict isohydric). Generally, evergreens were found to exhibit more negative maximum and greater diurnal variation of leaf water potential, greater wood density and lower water-use efficiency and leaf dry matter content than deciduous species but a surprising number of deciduous trees also showed impressive drought-tolerance. Semi-deciduous

leaf habits were less distinguishable due to a wide variety of trait combinations. No relationship was found between measured traits and growth form.

4. These findings contribute to a trait-based understanding of functional distributions along Neotropical dry forest climatic gradients by: (i) underscoring that trees employ similarly wide ranges of water-use behaviors across sites characterized by contrasting precipitation regimes and; (ii) leaf habit and stem count alone have limited utility as a way to classify dry forest species into ecologically meaningful groups.

KEY WORDS: tropical dry forest; functional traits; drought stress; stomatal responses; water potential; isohydric/ anisohydric behavior; trade-offs; plant hydraulics

INTRODUCTION

Anthropogenic climate change is thought to present a significant threat to tropical forests partly through the alteration of natural precipitation patterns (IPCC, 2014). This is of particular concern in forests that are already exposed to limited water resources and subject to extended annual dry seasons. Exceptional drought events have been linked to large-scale tree mortality (McDowell *et al.*, 2008) and disruption of key ecosystem processes including recruitment, nutrient cycles and plant growth (Schlesinger et al. 2016; Bonal et al. 2016). Tropical dry forests (TDFs) in the Neotropics, where functioning strongly relies on seasonal cycles of precipitation (seasonal drought often lasts ≥ 6 months) are expected to undergo more frequent and intense drought periods (Allen *et al.*, 2017). TDFs are known to exhibit resilience to occasional exceptional droughts for example by promoting the reestablishment of pioneer and colonizer species through shifts in seed production (O'Brien *et al.*, 2018). However, if intense droughts begin to occur at frequencies that do not allow forests to recover adequately, these biodiverse and carbon-rich systems may undergo a state change resulting in different structure and composition. One challenge in generalizing how TDFs will respond to climate change is the broad gradient in water availability they occupy, and the effect that has on ecological characteristics. Better understanding of plant adaptations to drought along gradients of mean annual precipitation (MAP) and seasonality will aid in quantifying functional shifts in water-use among TDFs and thus the wider response of these ecosystems moving into the future.

Long-term tree performance in TDFs is critically tied to water-use behavior during the dry season, which can vary widely in length and intensity both within and across sites. Such behaviors act to minimize the chances of drought-induced mortality due to hydraulic failure (Wang *et al.*, 2012), carbon starvation (Hartmann, 2011) or increased susceptibility to insect attack (Raffa *et al.*, 2008; Weed *et al.*, 2013). Over short timescales, regulation of stomatal conductance (g_s) is considered the primary mechanism through which plants can mitigate the combined effects of soil water desiccation and high atmospheric evaporative demand (VPD) by controlling gas-exchange at the leaf surface. By limiting excessive drops in leaf water potential (ψ_l), closure of stomata ensures that transpirational demands do not exceed the supply capacity of the hydraulic system (Martin-StPaul, 2017) which may lead to runaway embolism and whole-plant mortality. Such responses however come at a cost to photosynthesis, plant growth and regulation of leaf surface temperature (Ludlow, 1980).

Stomatal "strategies" can vary widely between coexisting species and have been described qualitatively as existing between two extreme categories: isohydric and anisohydric (Tardieu and Simonneau, 1998). In response to drought, isohydric plants close stomata rapidly in order to maintain a high ψ_l and limit vessel embolisms, but at the risk of carbon starvation. By contrast, anisohydric plants exhibit little stomatal control at low ψ_l, and therefore risk compromising hydraulic integrity and increasing chances of embolism formation. What is more likely however is that a continuum of behaviors exists between isohydric and anisohydric (Klein, 2014; Martinez-Vilalta *et al.*, 2014). It has been proposed that isohydric plants are generally favored in more mesic environments

allowing them to operate at water potentials very close to their hydraulic limits (Sperry, 1995). Other reports have suggested that among global biomes, the majority of species differ little in their rate of stomatal closure, and in fact it is the threshold ψ_l enacting stomatal control that changes due to differences between sites in drought intensity (Klein, 2014).

Previous attempts have been made to link physiological behaviors in water-use to morphological traits with the aim of gathering further insight into the coordinated trade-offs in resource economics that occur within the tropics (Markesteijn *et al.*, 2011b; Fu *et al.*, 2012; Lima *et al.*, 2012; Méndez-Alonzo *et al.*, 2013; Álvarez-Yépiz *et al.*, 2017). In TDFs these trade-offs have been largely defined by the need to acquire water efficiently and maintain xylem water transport to secure photosynthesis, while minimizing the risk of vessel cavitation and mortality (e.g. hydraulic efficiency vs. safety) (Tyree and Sperry, 1988; Engelbrecht *et al.*, 2007). As such, adaptations in hydraulic architecture are thought to explain a large portion of these trade-offs in TDFs. Indeed, water-use behavior has been found to be linked with wood density (Borchert, 1994; Singh & Kushwaha, 2005; Valdez-Hernandez *et al.*, 2010; Markestiejn *et al.*, 2011; Lima *et al.*, 2012). If a trade-off in hydraulic efficiency vs. safety does exist, it would be expected that species with traits conferring a greater degree of hydraulic efficiency would show stricter stomatal control (isohydric) through the need to balance efficient transport of water with protection of the xylem water column against cavitation.

Ultimately, categorizing species into ecologically meaningful groups based on dominant plant traits may offer the most practical route to simplifying TDFs for their use

in prediction models (Powers & Tiffin, 2010). One challenge is the spectrum of deciduous patterns (i.e. deciduous – intermediate – evergreen) TDF species exhibit (Sobrado, 1991) and their complicated association with hydraulic behaviors. The relatively low WD found among many tropical deciduous plants would suggest that during the dry season these species must limit transpirational loses to prevent embolism and therefore exhibit relatively constant ψ_l (isohydric behavior) and higher water-use efficiencies (WUE). That said, the ability of deciduous species to respond to drought may decline with leaf age and therefore species may show an increasingly anisohydric behavior with the subsequent decline in WUE and higher leaf water deficits being the catalyst for leaf drop. Alternatively, the ability to incrementally shed leaves may allow some deciduous trees to maintain isohydricy to reduce whole plant water stress and sustain rates of WUE for longer (Braga *et al.*, 2016). Overall, the precise relationship between leaf phenology and iso/anisohydric mechanisms remains unclear. Growth form may offer another avenue towards aggregating species based on their hydraulic properties. Indirect evidence has suggested that prolonged drought may be important in structuring TDFs by promoting the production of auxin and cytokinin which can initiate sprout development and stem production (Dunphy *et al.*, 2000; Van Bloem *et al.*, 2003). Short multi-stemmed shrubs may possess inherent advantages over single-stemmed trees in dry environments due to the insurance additional stems bring in the event of hydraulic failure (Espino & Schenk, 2009) and the reduced risk of cavitation in shorter stems under lesser gravitational constraints (Ryan & Yoder, 1997). There may be difficulty in directly comparing hydraulic properties between trees and shrubs however, as traits may covary

differently between growth forms. In a study of 200 woody species from across the Americas, trees had lower vessel density, and increased vessel diameters and height as well as overall higher degree of trait interrelatedness compared to shrubs (Martinez-Cabrera *et al.*, 2011).

Our aim was to evaluate the diversity of water-use strategies among 31 dominant TDF species in Puerto Rico. The dry forest zone experiences relatively low MAP and high rainfall unpredictability (low seasonality) relative to other Neotropical TDFs therefore we argue our work represents a valuable contribution to understanding trait distributions across precipitation gradients in Neotropical dry forest. We asked three questions and addressed the following hypotheses: 1) How do hydraulic strategies differ among TDF species? We hypothesized that the low seasonality index (high entropy of within-year rainfall) combined with low MAP likely act as a strong environmental filter for drought-adaptive traits and thus limit hydraulic trait variation at the community level; 2) How does water-use differ within plant functional groups relating to leaf habit and growth form? Traditionally higher SLA and low WD mean that during the dry season, deciduous species must limit transpirational loses to prevent embolism and therefore would exhibit relatively constant ψ_l (isohydric behavior) and higher WUE. Evergreens by contrast, through higher structural resistance can maintain relatively high rates of gas exchange despite the increased risk of cavitation (more anisohydric). We expected these leaf habit differences to fall along the traditional hydraulic efficiency vs. safety trade-off. Greater time lags in leaf drop among semi-deciduous and semi-evergreen species suggests these groups would show moderate levels of dehydration tolerance.

Additionally, we predicted that species associated with higher multi-stem rates would be related to traits associated with more liberal water-use due to their unique properties that help to offset the risk of hydraulic failure; 3) To what extent are morphological and physiological hydraulic properties related? We expected structural traits to be positively associated with ψ_l parameters and negatively related to g_s and WUE. Furthermore, we expected that higher stomatal density would be negatively associated with dry season g_{smax} as those species traditionally associated with higher rates of assimilation avoid drought effects. A strength of our study is that it utilizes two established approaches to evaluate the physiological behavior of plants during drought: 1) evaluating the extent of diurnal variation in ψ_l and the relationship between pre-dawn and midday ψ_l values (Martínez-Vilalta *et al.*, 2014) and; 2) using the relationship between simultaneous measurements of both ψ_l and g_s (Klein, 2014).

MATERIALS AND METHODS

STUDY AREA

Field research was conducted in the Guánica Dry Forest (17$_o$58'N, 65$_o$30'W), a 4400-ha biosphere reserve situated in the subtropical dry forest zone in southwest Puerto Rico. Prior to its protected status from 1919, the forest had a complex disturbance history including housing, charcoal cutting, goat raising and subsistence farming. Consequently, a mosaic of stands now exist that vary in structure and composition (Molina Colon & Lugo, 2006). Nevertheless, due to long-term protection Guánica is now recognized as one of the best examples of TDF in the Neotropics (Ewel & Whitmore, 1973).

Mean annual precipitation (MAP) is approximately 860mm but with high interannual variation, and mean annual temperature is 25.1°C (Murphy & Lugo, 1986b). Rainfall follows a bimodal distribution with an unpredictable early wet season (Apr-May) and a more consistent late wet season (August-November). Soils are relatively thin and alkaline (pH 7.8) having derived from calcareous parent material originating from the dominant limestone geology. As a result, phosphorus binds with calcium thereby decreasing overall bioavailability (Van Bloem *et al.,* 2004) which may explain why P-efficiency rates are some of the highest found worldwide (Lugo & Murphy, 1986). Slow annual decomposition rates result in a soil relatively rich in organic matter (23-30%) (Murphy & Lugo, 1986b).

Our study was conducted in the dominant upland semi-deciduous portion of the forest. Here evergreens make up ~50% of the community and coexist with drought-deciduous species although within valleys evergreen proportions are higher (Lugo *et al.,* 1978). Mean canopy height is 5-7m and the density of live stems (≥2.5m dbh) averages 12,000 stems per ha (Murphy & Lugo, 1986). Approximately 43.3% of trees are multi-stemmed (Dunphy *et al.*, 2000).

SPECIES SELECTION

We chose 31 dry forest tree species belonging to 18 families (Little & Wadsworth, 1964; Little *et al.*, 1974) (Table 1). Species were recognized dominants within upland Puerto Rican dry forest, and together represent over 87% of total trees ≥2.5cm dbh (Murphy & Lugo, 1986b). Almost all are considered native, except *Leucaena leucocephala*, an

introduced legume that often becomes dominant in disturbed areas (Molina Colon & Lugo, 2006). A continuum of leaf habits and multi-stemmedness were represented (Table 1). We defined semi-deciduous as those species that maintain much of their foliage long into the dry season until they typically shed all leaves once a threshold in drought is passed. However, time lags between species can vary considerably. Semi-evergreen species maintain and renew a full canopy year-round, except during strong drought when they can lose a considerable degree of foliage until drought conditions improve.

PHYSIOLOGICAL AND MORPHOLOGICAL TRAITS

Data were collected during two dry season phases between mid-2016 and mid-2017: 1) diurnal ψ_l measurements during the mid-summer 2016 dry season (July-Aug). This period represents the longest time elapsed since the late wet season when soil conditions can be considered driest due to ~6mo of inconsistent rainfall, mostly characterized by short episodic showers; 2) corresponding measurements of diurnal stomatal conductance (g_s) and leaf water potential (ψ_l) during the winter 2017 dry season (February). The g_s x ψ_l relationships of four deciduous species (*B. simaruba*, *P. unguis-cati*, *P. alba* and *T. portoricensis*) were measured in mid-summer 2017 as their canopies were bare in winter 2017. For each data collection phase, measurements were made on consecutive days between 04:00-16:00 at two-hour intervals, on 3-5 adult individuals per species. One value of Ψ_l was taken per tree using a pressure chamber (Model 1000, PMS Instrument Company, Albany OR) and three values of g_s were obtained per tree from the same three tagged leaves (abaxial side only) using an SC-1 steady state porometer (Decagon). All

leaves were fully developed, undamaged and collected under clear sunny skies. Bulk leaf samples from the same individuals were also collected during the 2017 winter dry season to measure ^{13}C composition ($\delta^{13}C$), a proxy for long-term WUE. Samples were dried at 75^{o}C for 72hr, ground and sent to the Duke DEVIL laboratory for analysis (*n*=5 per species). $\delta^{13}C$ was measured to an accuracy of +-0.01% using a Carlo Erba NA 1500 Elemental Analyzer.

We measured five leaf and stem traits on the same trees using standardized protocols (Cornelissen *et al.*, 2003) but included up to five additional trees nearby to improve sample sizes. All morphological trait data was collected during the 2016 mid-summer dry season (July-Aug). Leaves were allowed to rehydrate immediately following collection by storing them overnight in distilled water and in dark conditions. The next day, fresh mass was measured (precision balance ±0.001g) and leaves were scanned using a desktop scanner (Cannon MG3000, Tokyo, Japan). Leaf surface area (LA; cm^2) was measured using the freeware ImageJ (Schneider *et al.*, 2012; https://imagej.nih.gov/ij/index.html). Samples were then oven-dried at 75^{o}C for 72hr before dry mass was determined. The specific leaf area (SLA; $cm^2\ g^{-1}$) was calculated as leaf surface area/ dry mass. Leaf dry matter content (LDMC; $g\ g^{-1}$) was calculated as dry mass/fresh mass. To measure stomatal density (D_s; no. mm^{-2}), a film of clear nail polish was applied to both leaf surfaces on three leaves from each individual per species. Once dried, the film was removed, and impressions were mounted on slides and studied using a LEXT OLS4000 laser microscope (5X-100X) (Kröber *et al.*, 2015). For most species, stomata were counted from a leaf surface area of 417,315μm^2 but depending on the

clarity of stomata the area ranged from 67,340-1,643,520µm^2. All species concentrated their stomata on the abaxial (lower) surface providing the basis for D_s values. Wood density (WD; g g^{-1}) was determined from trees cores taken from 3-5 individuals from within the study area. Many species are considered very dense hardwoods, therefore we rehydrated cores inside a vacuum chamber for approximately one week to ensure full hydration. Fresh volume (without bark) was measured using the water displacement method (Ilic *et al.*, 2000). Cores were then dried for 96hr at 100^{o}C and dry mass was obtained using a precision balance (±0.0001g). Drying at 100^{o}C ensures complete evaporation of cell water prior to reweighing. WD was calculated as dry mass/ fresh volume.

STATISTICAL ANALYSIS

Species traits were ln-transformed when appropriate in order to improve normality and homoscedasticity. As LDMC is a proportionate trait, an arcsine-transformation was used. One-way ANOVA were used to determine mean differences in hydraulic traits including species and leaf habit as fixed factors. Where significant ($\alpha = 0.05$), Tukey HSD post-hoc tests were performed. We sought to determine physiological behaviors during drought in two ways: Firstly, a random slope linear mixed model (LMM) was used to fit the relationship between predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential (total unique observations *n*=209) (Martínez-Vilalta *et al.*, 2014). We added an additional fixed effect for leaf habit which improved our model fit. Species was a random effect, and the species-specific slopes of the model were allowed to vary. This model was used to infer

water-regulation behavior under increasingly drying conditions based upon using Ψ_{pd} as a proxy for soil water potential (Ψ_s). The slopes (σ) of the random effects coefficients (± 1SE) classified water-regulation within one of four categories: 1) strict isohydric ($\sigma \approx 0$; Ψ_l is maintained as Ψ_s drops); 2) partial isohydric ($0 < \sigma < 1$); 3) strict anisohydric ($\sigma = 1$); extreme anisohydric ($\sigma > 1$; the pressure drop within the plant continues to fall as Ψ_s decreases). Plots of the residual vs. fitted values as well as model residuals vs. all explanatory variables were examined to confirm assumptions of linearity, homoscedasticity and normality (Bates *et al.*, 2015; Zuur & Ieno, 2016).

Secondly, we plotted diurnal $g_s(\Psi_l)$ regression curves for all 31 species to directly assess stomatal behavior to drying conditions. Dixon tests were used to remove zero to five outliers from each curve (resulting in 14-30 points in given curves). No outliers were removed for 21 species. The species-specific functional response of g_s was determined using least-squares estimation and five functions were fitted based upon theoretical responses and used in past studies (Guyot *et al.*, 2012; Klein, 2014): linear ($g_s = a\,\psi_{leaf} + y_0$); quadratic ($g_s = c\,{\psi_{leaf}}^2 + b\,\psi_{leaf} + a$); logistic $\{g_s = \frac{a}{\left[1+\left(\frac{\psi_{leaf}}{x_0}\right)^b\right]}\}$; sigmoidal $\{g_s = \frac{a}{1+e^{-(\frac{\psi_{leaf}-x_0}{b})}}\}$; and exponential ($g_s = y_0 + ae^{-b\psi_{leaf}}$). Models were compared and selected based upon the lowest Akaike information criterion (AIC). Model diagnostics were performed to make sure assumptions of homogeneity, independence and normality were met.

Trait collinearity was assessed using PCA analysis with scaled mean trait values. Morphological traits were included as 'active' variables and physiological traits were

included *a posteriori* as supplementary variables. To explore relationships between physiological and morphological traits including the number of stems, in our context representing growth form, we used a Pearson's correlation analysis using species-specific mean trait values. We also calculated the degree to which hydraulic traits correlated with our first two PCA axes. All analyses were performed using 2016 mid-summer data except $g_s(\Psi_l)$ curves which used 2017 winter dry season data. Statistical analyses were conducted in R.3.5.2 (R Development Core Team, 2019).

RESULTS

WATER-REGULATION BEHAVIOR – Trees species fell along a continuum of behaviors exhibiting a comparatively large range of slope (σ) values and $g_s(\psi_l)$ patterns (Table 3.1; Fig. 3.1, see Table 3.2 for mixed model output). Overall, σ values ranged from -0.09 (strict isohydric) in *C. dodonea* to 1.15 (extreme anisohydric) in *T. portoricensis* (Table 3.1). Twenty-two species had σ values $0 < \sigma < 1$ (partial isohydric) however of these, 14 were >0.70 and in many instances close to 1 (we deem σ values close to one 1 as indicative of relatively anisohydric behavior as 1 represents the theoretical boundary between stomatal closure or hydraulic limitations having more effect on limiting transpiration). Eight species were categorized as anisohydric ($\sigma \geq 1$) suggesting hydraulic limitations were more influential on limiting transpiration than stomatal control.

Our analysis of stomatal behavior through $g_s(\psi_l)$ curves was complicated by the apparent variation in soil water availability between species (signified by the least

negative values of ψ_l on a given plot). Notably, a large number of our species displayed positive $g_s(\psi_l)$ relationships. Exclusively positive trends in $g_s(\psi_l)$ indicate that *in situ* drought conditions were not sufficient to initiate stomatal closure. Based on our findings, we grouped species into the following diurnal behaviors: 1) increase or maintenance of g_s, with peak conductance at relatively low ψ_l ($\geq$ -2.5MPa; n=12) (Fig. 3.1a & 3.1b); 2) increase or maintenance of g_s, with peak conductance at relatively high ψ_l ($\leq$ -2.0MPa; n=6) (Fig. 3.1c); 3) constant low rates of g_s, at highly negative ψ_l ($\geq$ -4.0MPa; n=6) (Fig. 3.1d); 4) high peaks in g_s early in the day (higher ψ_l) but continuing to maintain moderately high g_s throughout the day without full stomatal closure (n=2) (Fig. 3.1e); 5) negligible g_s throughout the day while maintaining a constant high ψ_l (n=3) (Fig. 3.1f). Two species (*T. portoricensis* and *E. areolatum*) had negligible g_s at very high ψ_l suggesting conditions were already too dry for these species to measure stomatal behavior.

At the leaf-habit level, evergreen species σ values were almost exclusively partial-isohydric (except *A. elemifera*), and 70% showed stomatal behavior akin to behavior 1 (see last paragraph; Fig. 3.1a). Deciduous species were more varied and could be separated into three general groups: 1) relatively anisohydric in σ values, and with stomatal behaviors #1 & #3; 2) relatively anisohydric in σ values and with stomatal behavior #2; 3) strongly isohydric ($\sigma < 0.50$) and dormant at high ψ_l (behavior #5; Fig. 3.1f). Interestingly, seven of our eight semi-deciduous species had remarkably similar σ values (range 0.85-0.88; partial-isohydric) but displayed many types of stomatal behaviors (#1-4). The one exception was the pioneer *C. dodonea,* a strict isohydric

according to our model ($\sigma \approx 0$) but capable of maintaining moderate g_s (c. 250mmol $m^{-2}s^{-1}$) at near constant ψ_l throughout the day. Semi-evergreens behaved very similarly to evergreens.

PHYSIOLOGICAL TRAITS – Physiological traits differed considerably among species, with interspecific differences responsible for 78.5% of the total variation in traits on average (range 67-92%; Table 3.3). ψ_{max} accounted for the largest variation among species, varying 5.5-fold respectively. Further, a large proportion of species achieved noticeably low dry season ψ_{max} including 13 species ≥-5.0MPa. Traits that explained the least amount of variation were ψ_{dv} and $\delta_{13}C$, differing 10- and 1.2-fold respectively. Dry season g_{smax} rarely exceeded 500mmol m^2s^1 other than for two deciduous legume species, *L. leucocephala* and *P. aculeata* (669 and 584mmol $m^{-2}s^{-1}$ respectively) and two semi-deciduous species of the same genus, *G. elliptica* and *G. krugii* (898 and 929mmol m^2s^1 respectively) (Appendix A). Deciduous species were segregated from other leaf habit groups with higher (less negative) ψ_{max} and $\delta_{13}C$ but lower ψ_{dv} (Fig. 3.3; Table 3.4). When legumes (Fabaceae) were analyzed separately, deciduous species also had the lowest g_{smax} (Table 3.4). Semi-deciduous and semi-evergreen strategies were generally more similar to evergreen than deciduous species but often were intermediate.

MORPHOLOGICAL TRAITS – Morphological traits differed markedly among species with species differences on average accounting for 84% of the total variation (range 70-94%; Table 3.3). D_s explained the greatest amount of variation among species (94%) and

LDMC the least (70%). Our ANOVA analysis indicated that all morphological traits but Ds were distinctly unique between leaf habits (Table 3.3). Deciduous and evergreen species were clearly segregated whereby deciduous species generally had higher SLA and LA, but lower LDMC and WD (Table 3.3). Evergreen and semi-evergreen species were found to be largely similar in all traits whereas semi-deciduous species were similar to deciduous species in SLA, WD and D_s and evergreen species in terms of LDMC, WD and D_s.

COLINNEARITY OF HYDRAULIC TRAITS – The first two principal components (PC) combined explained 64% of the trait variation (Fig. 3.3). PC1 explained 43% of the variation and was largely related to structural resistance (WD and LDMC were positively loaded) and optimization of WUE (SLA, LA and $\delta_{13}C$ were negatively loaded) which we interpret as evidence for the hydraulic safety-efficiency trade-off. PC2 explained an additional 21% of the variation and represented carbon-gain capacity grouping species with both high SLA and D_s. PC3 explained 15% of the variation and grouped species with high SLA and WD, but low D_s. ψ_{max} and ψ_{dv} correlated strongly and negatively with PC1, but no physiological traits correlated with our second or third axes. Significant opposite loadings were found along PC1 with deciduous species generally more hydraulically efficient (-0.89, $p< 0.001$) and evergreens favoring safety (1.43, $p< 0.01$) (Fig. 3.3). There was no leaf habit association with PC2. Evergreen species were correlated with PC3 (loading of 0.42, $p<0.05$). Intermediate strategies occupied small loadings and shared much overlap with evergreen and deciduous species. Although not

statistically significant, the two semi-evergreen species occupied the same zone as true evergreen species whereas semi-deciduous species were well dispersed throughout multidimensional trait space.

RELATIONSHIPS BETWEEN PHYSIOLOGICAL AND MORPHOLOGICAL TRAITS - We observed similar correlations between the two ψ_l parameters and a number of morphological traits (Table 3.5; Fig. 3.4). ψ_{dv} showed a strong relationship with LDMC (r^2 = -0.66, p<0.001) as well as a moderate relationship with LA (r^2 = 0.45, p<0.01; Table 3) and WD (r^2 = -0.35, p<0.05). ψ_{max} exhibited strong negative correlations with WD (r^2 = -0.53, p<0.01) and LDMC (r^2 = -0.51, p<0.01) and moderate positive correlations with LA (r^2 = 0.45, p<0.01; Table 3.5). $\delta_{13}C$ displayed moderate-weak relationships with LDMC (r^2 = -0.36, p<0.05) and D_s (r^2 = -0.39, p<0.05). No relationships were found between morphological traits and g_{smax}.

DISCUSSION

DIFFERENCES IN WATER-USE AMONG TROPICAL DRY FOREST TREES

We hypothesized that low MAP and relatively indistinct seasonality would limit trait variability and select toward species with highly drought-adaptive traits. Previous studies in TDFs defined by low precipitation, distinct seasonality, and different substrates have shown a broad range of water-use behaviors among species ranging from conservative to acquisitive and drought avoidant to drought tolerant (Pineda-Garcia *et al.*, 2011; Aguilar-

Romero *et al.*, 2017; Alvarez-Yépiz *et al.*, 2017; Werden *et al.*, 2018). Considering the relatively few studies in TDFs defined by both low MAP and low seasonality index, gaps remain in our understanding of water-use behaviors exhibited by tree species subject to such conditions.

Strikingly, our dataset identified a broad spectrum of dry season water-use behaviors among our 31 species. The large interspecific variation in ψ_l parameters, σ values from our linear model, and the range of $g_s(\psi_l)$ curves suggests that the forest community is comprised of species that possess multiple drought-adaptation strategies. Such variety in behaviors may not be surprising considering the unpredictable nature of rain in the ecosystem. A high diversity in tree ecological strategies has been found within communities occupying a range of precipitation environments and has been used as a strong basis for niche diversity (Grime, 2001; Wright *et al.*, 2004; Ackerly & Cornwell, 2007; Reich, 2014).

Included in the variability of water-use behaviors were a large proportion of markedly dehydration tolerant species. Although the mid-summer 2016 LMM identified species that were mildly sensitive to declining Ψ_s (partial-isohydric but σ values close to 1), few appeared to close stomata in winter 2017 when diurnal drought stress peaked around noon. The anisohydric species similarly exhibited little stomatal sensitivity under mid-summer 2016 conditions, but their steep σ values ≥ 1 suggest that rather than reducing stomatal aperture, internal hydraulic limitations (e.g. initiation of embolisms in the xylem) may act as the mechanism that would cease gas-exchange (Martínez-Vilalta *et al.*, 2014). These results indicate a common strategy of maintaining carbon assimilation

and transpiration under relatively stressful dry season conditions, perhaps unsurprising considering annual growth rates are low in Guánica (Murphy & Lugo, 1986b). Such species may possess adaptive traits that allow dry season access to water such as deep or dimorphic root systems (Oliveira *et al.*, 2005; Liu *et al.*, 2014) and in this regard the effects of drought may be beneficial as greater water deficits can aid species to extract water from drier and deeper soils (Holbrook *et al.*, 1995). Indeed, the high root:shoot ratio (0.5) observed in Guánica Forest (Murphy & Lugo, 1986b) suggest extensive root systems are common here. Osmotic adjustment has also been widely reported in TDF species as a mechanism to assist the maintenance of turgor by offsetting large declines in ψ_l and allowing continued dry season g_s (Sobrado, 1986; Eamus, 1999; Garcia-Nunez *et al.*, 2019). Consistent with lower osmotic potentials were numerous species including *G. lucida* (Fig. 1d) that continued to maintain partial stomatal opening despite highly negative ψ_l ($\geq$ -4.0MPa).

The lack of relatively strict isohydric species was unexpected considering that strong stomatal sensitivity seems advantageous during the dry season when extended drought periods and high VPD may increase the potential for runaway cavitation and death (McDowell *et al.*, 2008; O'Brien *et al.*, 2017). Based on established theory, peak g_s could be expected at higher ψ_l (i.e. earlier morning or late afternoon) when VPD is moderate and WUE can be maximized (see Optimization model of stomatal regulation; Cowan & Farquhar, 1977). Only two of our species exhibited this pattern (*G. elliptica* and *G. krugii*). An unpredictable rainfall environment may select for a higher proportion of anisohydric and weak isohydric species. During the early wet season and mid-summer

dry season in our TDF (Mar-Aug), rainfall generally occurs as short irregular pulses (Allen *et al.*, 2017) that tend to only affect upper soil layers. Therefore, drought during this time is characterized as long but less intense than if seasonality was more distinct (drought would be shorter but more intense). "Carbon starvation" may be more likely for strict isohydric species during long drought periods as photosynthesis would be limited while stomata are closed (McDowell *et al.*, 2008), a theory consistent with our identification of only three strict isohydric species (*B. simaruba*, *P. alba* and *C. dodonea*; Fig. 3.1f). Additionally, strict isohydricy likely inhibits evaporative cooling and increases susceptibility to pathogenic attack from reduced carbon acquisition (Ayres & Lombardero, 2000; Meir *et al.*, 2006).

Other studies of large taxonomic sets in Neotropical TDF have found a tendency for species to favor dehydration tolerance over avoidance. In northwestern Costa Rica where more distinct seasons and higher MAP occurs (1765mm, 30-yr mean), no tree species exhibited strict isohydricy, whereas eight species showed extreme anisohydric behavior and six were partial isohydric although specific σ values were not reported (Werden *et al.*, 2018). Together with our results, these data suggest tree species characterized by dehydration tolerance may be more abundant than dehydration avoiders across gradients in MAP and seasonality within Neotropical TDFs.

Instances among species where LMM coefficients conflicted with $g_s(\psi_l)$ regression curves demonstrate the challenge of interpreting physiological behaviors across dry seasons.

For example, the σ coefficient of *R. guama* was 0.62 (suggesting stomata were relatively sensitive to soil desiccation) however, the $g_s(\psi_l)$ curve (see Appendix B) showed *R. guama* operating at surprisingly high g_s at highly negative ψ_l. Our findings are likely connected to the variation in drought dynamics between winter and mid-summer dry seasons. Drought is likely less severe in the winter due to legacy effects of the preceding late wet season including groundwater recharge that aids deep-rooted species to counteract daytime transpiration with overnight refilling. Physiological changes related to leaf ontogeny may also affect leaf-level processes. Overall, it's important to consider the contribution of trait plasticity, for example here reflected in the temporal adjustment of stomatal sensitivity, on changes in interspecific water-use.

The correlation of leaf water potential parameters (ψ_{max} and ψ_{dv}) along PC1 indicates that much of the segregation between isohydric and anisohydric behaviors can be explained by investment for leaf and stem structural resistance. Higher WD and LDMC are both associated with higher fiber-wall thickness and denser cell packing, both which are known to be linked to resistance to xylem embolism (Hacke *et al.*, 2001; Chave *et al.*, 2009, Tng *et al.*, 2018). As such, these traits may allow dehydration tolerant species to withstand the high negative xylem pressure imposed by transpirational stresses and hence maintain partial g_s later into the dry season when high VPD is matched with greater soil water deficits. Of those anisohydric species that appear to rely upon the onset of hydraulic transport limitations to reduce transpiration rather than stomatal closure ($\sigma \geq 1$), recovery by refilling of cavitated conduits via dissolution may necessitate narrow conduits typically found in dense wood (Sperry, 1995). In contrast, many of the species

that maintained higher ψ_{max}, constant ψ_{dv} and negligible g_s possessed less cavitation resistant leaves and wood but higher WUE and carbon gaining capacity. For these isohydric species, intermittent periods of dormancy throughout the year are likely common and therefore the ability to maximize carbon acquisition when environmental conditions improve is desirable. Strict stomatal control combined with the greater water storage capacity of their low density stems acts to maintain high relative leaf water content (Holbrook *et al.*, 1995), counteracting the effects of ongoing cuticular conductance prior to leaf abscission.

RELATIONSHIP BETWEEN HYDRAULIC STRATEGIES AND PLANT FUNCTIONAL GROUPS

Previous studies within semi-arid ecosystems have attempted to shed light on whether distinct water-use behaviors are linked to tree species with different life history strategies (e.g. leaf habits or successional status) or growth form (e.g. trees vs. woody vines or shrubs) based upon the segregation of physiological and morphological traits (Sobrado, 1986; Markesteijn *et al.*, 2011; Fu *et al.*, 2012; Pineda-Garcia *et al.*, 2015; Alvarez-Yépiz *et al.*, 2016; Werden *et al.*, 2018). For example, deciduous vs. evergreen species have been shown to differ in their stem and leaf hydraulic conductivities (Markesteijn *et al.*, 2011) as well as hydraulic efficiencies and turgor loss points (Sobrado, 1986; Fu *et al.*, 2012). Single-stemmed trees have shown a tight association between wood density and vessel parameters but for multi-stemmed shrubs the same traits show differing degrees of independence (Martinez-Cabrera *et al.*, 2011). Our study extends previous efforts by

integrating intermediate leaf habit groups that better represent the broad range of phenological behaviors present in TDF and using the mean number of stems for a species as a metric that describes the diversity of structural forms between trees and shrubs (Götmark *et al*., 2016).

Species in our study with distinct leaf habits exhibited differences in dry season water-use, specifically between true deciduous and true evergreen species. True deciduous species showed a greater range in behaviors (partial isohydric to extreme anisohydric) but on average maintained more constant ψ_{dv}, higher ψ_{max} and a greater degree of stomatal closure at higher ψ_l which also helps to explain the greater WUE we observed in deciduous species relative to evergreens. These results are consistent with segregation in water-use strategies between deciduous and evergreens described elsewhere in the seasonally dry tropics (Sobrado, 1991; Prior *et al.*, 2003). Lower dry season osmotic potentials and inelastic cell walls possessed by evergreens allow leaf turgors to be sustained over greater declines in water potential, thus maintaining cellular function and relatively high g_s as drought proceeds (Sobrado, 1986; Fanjul & Barradas, 1987). Deciduous species that were more isohydric on average exhibited greater carbon-gain capacity (higher SLA and LA) and lower WD and LDMC, suggesting larger vessels that are more vulnerable to cavitation (Rosner, 2017). Overall, these results align with the presence of a hydraulic efficiency/safety trade-off which was evident by the significant relationships true deciduous and true evergreen groups had along PC1 of our PCA analysis and has been well documented in other arid environments (Pockman & Sperry, 2000, De Guzman *et al.*, 2017). Other TDFs have shown deciduous species to

consistently be more vulnerable to cavitation and invest less in hydraulic structure than co-occurring evergreens (Sobrado, 1993; Choat *et al.*, 2005; cf. Brodribb *et al.*, 2003). Nevertheless, we note the large variability in physiological behaviors and morphological traits among true deciduous species, particularly in their WD. Other semi-arid sites with low, unpredictable rainfall have shown similar variety in deciduous stem structure and its relation to drought tolerance (Lima *et al.*, 2012). We were not able to link intermediate leaf habits to distinct water-use strategies as they broadly overlapped trait space with true deciduous and true evergreen species. Semi-evergreen species in particular were found to be very similar to evergreens suggesting their distinction as a separate group is redundant. Ultimately, intermediate groups embody a large range of abscission, emergence and reproductive dynamics which may contribute to the range of physiological behaviors and traits they appear to show.

The high intra-group diversity and significant overlap between groups we observed suggests limitations of linking hydraulic traits to leaf habit. Such patterns may not always be clear when investigating small groups of taxa that represent the tail ends of trait distributions. Importantly, our taxonomically diverse group of 31 species represents a high degree of phylogenetic independence (Muscarella *et al.*, 2014) and a major portion of the TDF community in Puerto Rico (close to 90% of the total individuals in Guánica; Murphy & Lugo, 1986b). Previous TDF research involving large taxonomic groups has had mixed success in defining hydraulic properties by leaf habit. Among 40 species in the slightly wetter (1160mm MAP) eastern lowlands of Bolivia, deciduous and evergreen species differed in their hydraulic conductivities and WD, but interestingly not in ψ_{max},

and a similar lack of difference was found for xylem tension at 50% loss of hydraulic conductivity among 13 species in the same forest (Markesteijn *et al.*, 2011a; Markesteijn *et al.*, 2011b). Similarly, Powers & Tiffin (2010) defined the trait distributions of 87 species in northwestern Costa Rica (1575-1700mm MAP) but found no meaningful differences between leaf habits were found for traits including SLA, WD, leaf chemical composition and $\delta_{13}C$ (other than for legumes). Notably, similar to our study the authors made the distinction between true deciduous and semi-deciduous habits.

Leaf habit as part of a more complex approach to classifying TDF species may have promise in determining ecologically meaningful groups. For example, based on 37 TDF species in the relatively wet (1240 ± 385mm) and seasonally distinct Guanacaste province of Costa Rica, Borchert (1994) suggested clustering trees according to leaf habit and WD, due to variations in stem water storage capacity and species occurrence along a local gradient in water availability. Specifically, a diverse group of deciduous species including those with high wood density and low-density water-storing species performed well in dry upland sites whereas low-density evergreens tended to dominate the moist lowland areas where plants had continued access to the water table. Similar species combinations have been found in a dry forest with similarly distinct seasons but lower MAP in Chamela, Mexico (Mendez-Alonzo *et al.*, 2013). Such findings are largely consistent with the high trait diversity among deciduous species in our upland plots and suggests that the driest TDF sites may select for a wider spectrum of hydraulic strategies representing the adaptive evolution of species in response to abiotic stressors. Dense, dehydration-tolerant evergreens that appeared to thrive in Puerto Rican upland areas

occur in other wetter TDF sites (Choat *et al.*, 2006; Markesteijn *et al.*, 2011b; Fu *et al.*, 2012); however, based on Neotropical TDF site comparisons Guánica appears to have a relatively high proportional make-up of evergreens within the local community (~50%; Vargas *et al.*, *unpublished*). In this respect, our forest shares similarities to Neotropical savannas where high-WD, dehydration-tolerant evergreens are known to be relatively common (Sarmiento *et al.*, 1985; Lima *et al.*, 2012).

Drought has been shown to promote sprouting of dormant buds, which can lead to higher numbers of stems (Kolb & Davis, 1994; Dunphy *et al.*, 2000). We found limited evidence for relationships between multi-stem rates and hydraulic traits other than species with a higher number of stems (more shrub-like) were found to have higher leaf structural resistance (LDMC). Higher fiber content acts as an important mechanism of hydraulic resistance which may aid in the favorable distribution of multi-stemmed individuals in drier sites. None of our species were strictly shrubs, which may explain the contrast to Martinez-Cabrera *et al.* (2011), who found significant differences between trees and shrubs in the degree of association between hydraulic traits. Further, the evolutionary effect of hurricanes on tree growth form in the Caribbean may confound our findings as these events increase the abundance of facultative-sprouters. Obligate and facultative sprouters may be defined by similar stem rates but occupy different resource niches and thus differ in their trait assemblages.

RELATIONSHIPS BETWEEN PHYSIOLOGICAL AND MORPHOLOGICAL TRAITS

Our results are consistent with those from other Neotropical TDF environments and thus together suggest relationships between physiological and morphological traits extend across a MAP gradient from relatively wet Costa Rican TDF (~1765mm; Werden *et al.*, 2018), moderately wet Brazilian cerrado (~1500mm; Gotsch *et al.*, 2010) to drier lowland deciduous forests in Bolivia (~1160mm; Markesteijn *et al.*, 2011) and Puerto Rico. Wood density and LDMC were negatively correlated with ψ_{max} and ψ_{dv} which is in agreement with their established role in drought adaptation (Chave *et al.*, 2009, Kursar *et al.*, 2009). WD is an informative hydraulic trait as conduit space dedicated to sap flow is dependent on tissue density (Chave *et al.*, 2009) although some studies among angiosperms have demonstrated mixed results linking WD to vessel anatomy (Preston *et al.*, 2006, Pratt *et al.*, 2007). Withstanding high negative pressures is connected to the hydraulic architecture associated with dense wood. As cell wall thickness is thought to remain constant with lumen diameter (Zanne *et al.*, 2010), the greater cell packing found in the narrow vessels of dense wood results in a higher cell wall to lumen ratio (Hacke *et al.*, 2001; Rosner, 2017). As a result, vessel implosions due to high negative xylem pressures are less likely. Interestingly, Markesteijn *et al.* (2011) found similar relationships among saplings of 40 species indicating that the coordination of leaf and stem traits also remains coupled across ontogenies (cf. Baraloto *et al.*, 2010).

Long-term WUE was weakly related to LDMC which can be attributed to differences in dry season gas-exchange along the spectrum of isohydric and anisohydric behaviors. Lower LDMC is generally associated with a greater need to avoid the effects of drought by increasing stomatal sensitivity (more isohydric). When stomata are closed and g_s is

low, little fractionation of the ^{13}C isotope can occur as almost all intercellular CO_2 must react with RuBP carboxylase resulting in higher WUE (Farquhar *et al.*, 1989). By contrast, when dehydration tolerance allows for a relatively high g_s, discrimination between ^{12}C and ^{13}C during photosynthesis is greatest. The weak negative correlation between long-term WUE and D_s is somewhat surprising in the context of water-regulation in dry environments. Although we did not measure stomatal size, theoretical packing limits on the leaf surface suggest that greater D_s is generally matched by smaller stomata. Smaller stomata have been linked to faster stomatal response times (Hetherington & Woodward, 2003; Franks & Farquhar, 2007) in order to optimize water-use and carbon gain in drought environments. Considering many species exhibited relatively weak stomatal control within our study, we propose that biophysical constraints of diffusion through pores may be influential whereby smaller stomata are able to provide higher g_s for the same total pore area due to shorter diffusion path lengths (Franks & Beerling, 2009).

CONCLUSION

The impressively large variety of water-use behaviors observed in Puerto Rican TDF suggests that the variation previously observed in sites characterized by higher MAP and more distinct seasonality extends to much drier, unpredictable TDF environments. The relative abundance of species considered extremely dehydration-tolerant was high relative to other sites. In our site, much of a plant's response could be explained through a combination of leaf and stem structural investment and leaf habit – but generally only for

true deciduous and true evergreen species. The multitude of semi-deciduous species did not consistently exhibit similar trait relationships, instead these species had a variety of combinations of leaf habit, morphological, and physiological traits. As such, these findings lend further support that leaf habit alone is insufficient to classify species according to their water-use behavior in dry forest environments. The wide variety of trait combinations appears to mirror a highly variable rainfall environment, where amount and timing of annual rainfall, length and onset of seasonality, and size of rainfall events are all highly variable.

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TABLES

Table 3.1. The 31 tree species for which hydraulic properties were measured. Mean stems per tree obtained from both personal data and Van Bloem *et al.* (2003). Water-regulation classifications and slope coefficients based on a linear model of the relationship between predawn and midday water potential. Slope confidence intervals based on ±1SE. Leaf habit abbreviations include: DEC, deciduous; SDEC, semi-deciduous: SEG, semi-evergreen; EG, evergreen. †also has photosynthetic bark.

Species	Family	Leaf-habit	Mean no. stems	Water-regulation (slope ± 1SE)
Amyris elemifera	Rutaceae	EG	1.5	Strict anisohydric (0.93 ± 0.07)
Bourreria succulenta	Boraginaceae	SDEC	1.5	Partial isohydric (0.88 ± 0.07)
Bucida buceras	Combretaceae	SDEC	2.3	Partial isohydric (0.85 ± 0.07)
Bursera simaruba†	Burseraceae	DEC	1.0	Partial isohydric (0.35 ± 0.23)
Coccoloba diversifolia	Polygonaceae	EG	3.1	Partial isohydric (0.33 ± 0.07)
Coccoloba microstachya	Polygonaceae	SDEC	6.1	Partial isohydric (0.86 ± 0.07)
Colubrina arboreceans	Rhamnanceae	DEC	2.4	Strict anisohydric (0.95 ± 0.07)
Comocladia dodonea	Anacardiaceae	SDEC	3.7	Strict isohydric (-0.09 ± 0.14)
Crossopetalum rhacoma	Celastraceae	SEG	2.5	Partial isohydric (0.63 ± 0.08)
Elaeodendrum xylocarpa	Celastraceae	EG	1.6	Partial isohydric (0.49 ± 0.08)
Erithalis fruiticosa	Rubiaceae	EG	4.4	Partial isohydric (0.57 ± 0.07)
Erithroxylon areolatum	Erythroxylaceae	DEC	1.2	Strict anisohydric (0.96 ± 0.07)
Erithroxylon rotundifolium	Erythroxylaceae	SDEC	2.3	Partial isohydric (0.85 ± 0.07)
Eugenia foetida	Myrtaceae	EG	1.4	Partial isohydric (0.87 ± 0.07)
Eugenia rhombea	Myrtaceae	EG	2.5	Partial isohydric (0.72 ± 0.07)
Exostema caribaeum	Rubiaceae	DEC	1.2	Strict anisohydric (1.06 ± 0.08)
Guettarda elliptica	Rubiaceae	SDEC	6.4	Partial isohydric (0.88 ± 0.07)
Guettarda krugii	Rubiaceae	SDEC	3.4	Partial isohydric (0.87 ± 0.07)
Gymnanthes lucida	Euphorbiaceae	EG	1.5	Partial isohydric (0.71 ± 0.07)
Jacquinia berteroi	Theophrastaceae	EG	4.1	Partial isohydric (0.31 ± 0.10)
Krugiodendron ferreum	Rhamnaceae	EG	1.2	Partial isohydric (0.73 ± 0.07)
Leucaena leucocephala	Fabaceae	DEC	1.3	Strict anisohydric (1.08 ± 0.09)
Mosiera xerophytica	Myrtaceae	SEG	6.4	Partial isohydric (0.79 ± 0.08)
Pictetia aculeata	Fabaceae	DEC	2.4	Partial isohydric (0.90 ± 0.07)
Pisonia albida	Nyctaginaceae	DEC	1.6	Partial isohydric (0.80 ± 0.10)
Pithocellobium ungis-cati	Fabaceae	SDEC	7.2	Partial isohydric (0.86 ± 0.07)
Plumeria alba	Apocynaceae	DEC	1.2	Partial isohydric (0.49 ± 0.11)
Reynosia vivesiana	Rhamnaceae	EG	6.0	Partial isohydric (0.62 ± 0.07)
Tabebuia heterophylla	Bignoniaceae	DEC	6.5	Strict anisohydric (1.03 ± 0.10)
Thouinia portoricensis	Sapindaceae	DEC	4.2	Extreme anisohydric (1.15 ± 0.07)
Zanthoxylum flavum	Rutaceae	DEC	1.5	Strict anisohydric (0.94 ± 0.07)

Table 3.2. Linear mixed model results for the relationship between midday leaf water potential and the fixed-effect parameters of pre-dawn leaf water potential and leaf habit. Significant relationships: *, 0.05> *p*> 0.01; **, 0.01> *p*> 0.001; ***, *p*< 0.001; ns, not significant. The lmer function in R uses Satterthwaite approximations to degrees of freedom to calculate t-tests. Confidence intervals are provided via Wald approximations (confidence level = 0.95).

Explanatory variables	Coefficient ± SE	*t*-value	Lower CI (2.5%)	Upper CI (97.5%)
Intercept	-0.81 ± 0.13	-6.19***	-1.079	-0.556
Predawn leaf water potential (ψ_{pd})	0.75 ± 0.06	12.23***	0.610	0.879
Leaf habit (evergreen)	-1.65 ± 0.19	-8.48***	-2.068	-1.241
Leaf habit (semi-deciduous)	-0.63 ± 0.20	-3.17**	-1.052	-0.228
Leaf habit (semi-evergreen)	-0.97 ± 0.31	-3.15**	-1.581	-0.363
	Model AIC = 251.84; r_2 (fixed-effects) = 0.63 r_2 (total) = 0.96			

Table 3.3. Among-species variation in hydraulic properties for 31 TDF species, indicated by one-way ANOVA. Results include degrees of freedom (DF); sums of squares (SS); mean sums of squares (MS); *F-ratio* and significance (*p*); amount of variation explained by among-species differences (adjusted-r^2; %); mean trait value (±SE); minimum (Min) and maximum (Max) trait values; and the max:min ratio. *** significance $p < 0.001$. Traits were ln-transformed except LDMC (arscine), $\delta^{13}C$ and WD.

	DF	SS	MS	*F*	*p*	r^2 (adj)	Mean ± SE	Min	Max	Ratio
Physiology										
Maximum leaf water potential (ψ_{max}; MPa)	30	46.16	1.54	77.28	***	92	-3.65 ± 0.21	-1.04	-5.71	5.49
Diurnal variation in leaf water potential (ψ_{dv}; MPa)	30	77.11	2.57	14.92	***	67	-0.97 ± 0.08	0.19	-1.88	-10.02
Maximum stomatal conductance (g_{smax}; mmol m^{-2} s^{-1})	30	84.16	2.81	35.33	***	88	308.99 ± 39.76	50.36	929.29	18.45
Long-term water-use efficiency ($\delta^{13}C$; ‰)	30	178.37	5.95	11.47	***	67	-27.65 ± 0.20	-25.22	-29.44	1.17
Morphology										
Specific leaf area (SLA; cm^2 g^{-1})	30	21.34	0.71	35.53	***	81	90.69 ± 4.71	37.05	147.20	3.97
Leaf dry matter content (LDMC; g g^{-1})	30	1.49	0.05	20.22	***	70	0.43 ± 0.01	0.23	0.55	2.34
Leaf area (LA; cm^2)	30	222.26	7.41	77.66	***	90	25.14 ± 5.36	1.57	117.90	74.94
Wood density (WD; g g^{-1})	30	4.42	0.15	24.76	***	84	0.81 ± 0.03	0.25	1.17	4.66
Stomatal density (D_s; no. mm^2)	27	42.09	1.56	70.23	***	94	271.78 ± 33.56	80.08	798.22	9.97

Table 3.4. Mean differences between leaf habit groups including one-way ANOVA results (with leaf habit as a fixed factor). * legumes analysed as a separate life-history group. Lowercase letters after mean values indicate results from Tukey's post-hoc significant comparisons. Leaf habit groups that do not share letters are statistically different from one-another. Significance: *, p <0.05; **, p <0.01; ***, p <0.001. Trait and ANOVA abbreviations as in Table 3.3.

	Deciduous	Evergreen	Semi-deciduous	Semi-evergreen	Fabaceae	One-way ANOVA				
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	DF	SS	MS	*F*	*p*
Physiology										
ψ_{max} (-MPa)	3.46 ± 0.20 a	4.67 ± 0.15 b	4.49 ± 0.17 b	3.53 ± 0.19 ab	NA	3	6.82	2.27	10.72	***
ψ_{dv} (-MPa)	0.68 ± 0.06 a	1.33 ± 0.08 c	1.05 ± 0.05 b	1.06 ± 0.13 bc	NA	3	18.44	6.15	13.86	***
g_{smax} (mmol m^{-2} s^{-1})	252.20 ± 29.40	271.75 ± 20.34	347.92 ± 53.62	306.28 ± 34.24	NA	3	12.47	4.16	1.25	ns
g_{smax}* (mmol m^{-2} s^{-1})	204.12 ± 23.92 a	271.75 ± 20.34 ab	392.42 ± 58.46 b	306.28 ± 34.24 ab	400.80 ± 80.41 ab	4	6.56	1.64	2.7	*
$\delta_{13}C$ (‰)	-27.06 ± 0.19 b	-28.11 ± 0.15 a	-27.74 ± 0.17 a	-28.22 ± 0.17 a	NA	3	32.73	10.91	7.78	***
Morphology										
SLA (cm g^{-1})	104.66 ± 2.95 b	70.87 ± 2.17 a	100.71 ± 2.77 b	71.75 ± 4.37 a	NA	3	8.44	2.81	39.45	***
LDMC (g g^{-1})	0.38 ± 0.01 a	0.46 ± 0.01 b	0.44 ± 0.01 b	0.44 ± 0.01 ab	NA	3	0.37	0.12	18.25	***
LA (cm^2)	44.99 ± 4.40 c	10.50 ± 0.81 a	16.37 ± 1.21 b	8.36 ± 1.84 a	NA	3	89.47	29.8	46.91	***
WD (g g^{-1})	0.75 ± 0.04 a	0.86 ± 0.02 b	0.81 ± 0.02 ab	0.87 ± 0.07 ab	NA	3	0.32	0.11	3.01	*
D_s (no. mm^2)	220.45 ± 17.15	331.15 ± 29.69	285.80 ± 38.04	240.96 ± 28.14	NA	3	2.14	0.71	2.05	ns

Table 3.5. Bivariate relationships between physiological and morphological hydraulic traits of 31 TDF species. Bivariate relationships were calculated using Pearson's coefficients. The mean number of stems (NoStems) was not included in the PCA analysis. Significance: *, p <0.05; **, p <0.01; ***, p <0.001, all others non-significant. Abbreviations found in Table 3.3.

	ψ_{max}	ψ_{dv}	g_{smax}	$\delta_{13}C$	WD	SLA	LDMC	LA	D_s	NoStems
Water-balance										
ψ_{max}										
ψ_{dv}	**0.51****									
Gas-exchange										
g_{smax}	-0.17	-0.26								
$\delta_{13}C$	-0.19	0.30	0.14							
Stem traits										
WD	**-0.53****	**-0.35***	0.07	-0.10						
Leaf traits										
SLA	-0.02	0.23	-0.15	0.06	-0.20					
LDMC	**-0.51****	**-0.66*****	0.16	**-0.36***	**0.45****	**-0.35***				
LA	**0.37***	**0.45****	-0.20	0.22	-0.17	**0.46****	**-0.48****			
Ds	-0.22	-0.18	-0.06	**-0.39***	0.27	0.07	0.03	-0.07		
Growth form										
NoStems	-0.01	-0.01	0.11	-0.08	0.19	-0.31	**0.48****	-0.25	-0.09	
PCA										
Axis 1	**-0.54****	**-0.60*****	-0.06	**0.30***	**-0.69*****	**0.59*****	**-0.81*****	**0.78*****	-0.22	NA
Axis 2	-0.23	-0.04	0.08	0.21	-0.25	**-0.45****	0.13	0.01	**-0.89*****	NA

FIGURES

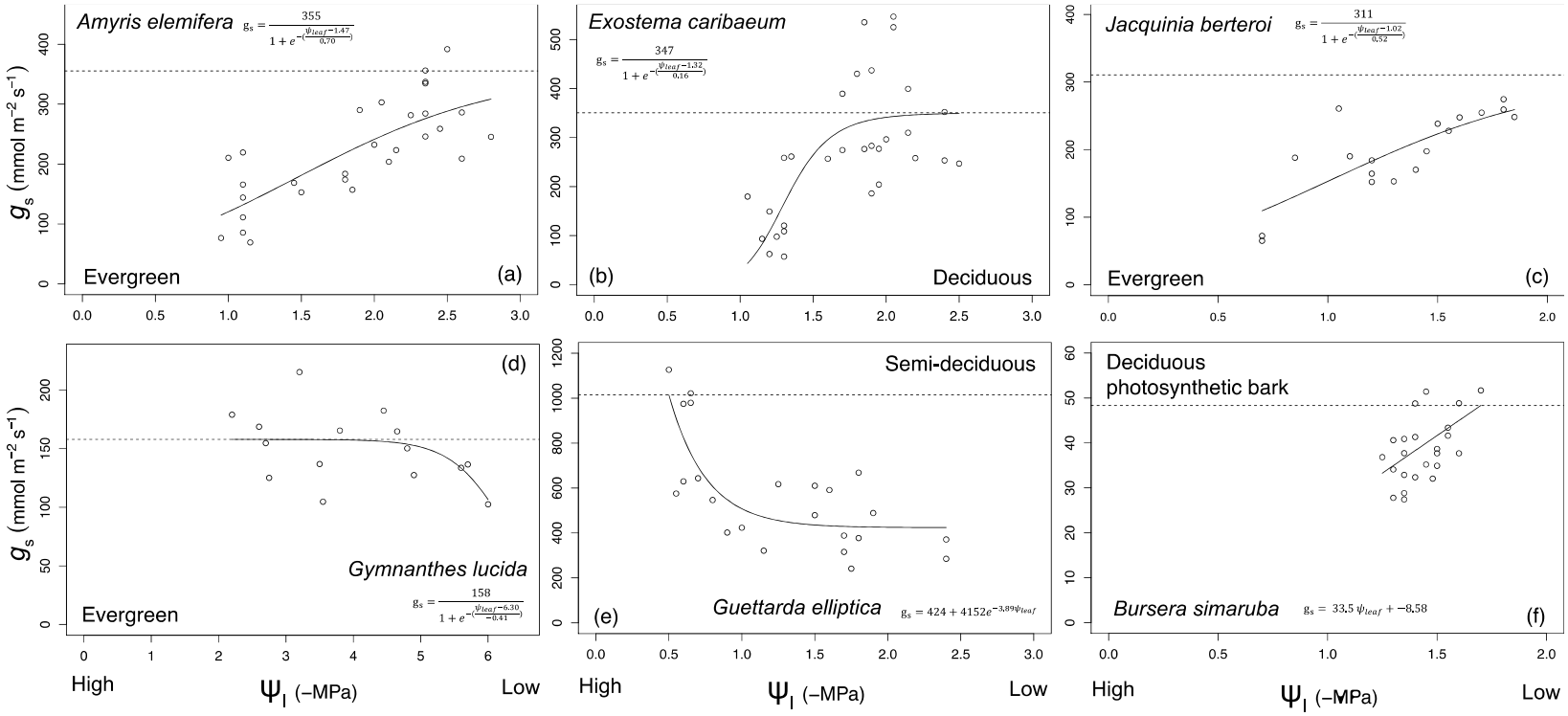

Figure 3.1. Regression curves of the response of stomatal conductance (g_s) to leaf water potential (ψ_l) for six species that illustrate different behaviors in response to soil desiccation. Species-specific curve equations are included. Dashed horizontal lines represent the fitted maximum for g_s. Note scales are not uniform among panels. All species are presented in supplementary information.

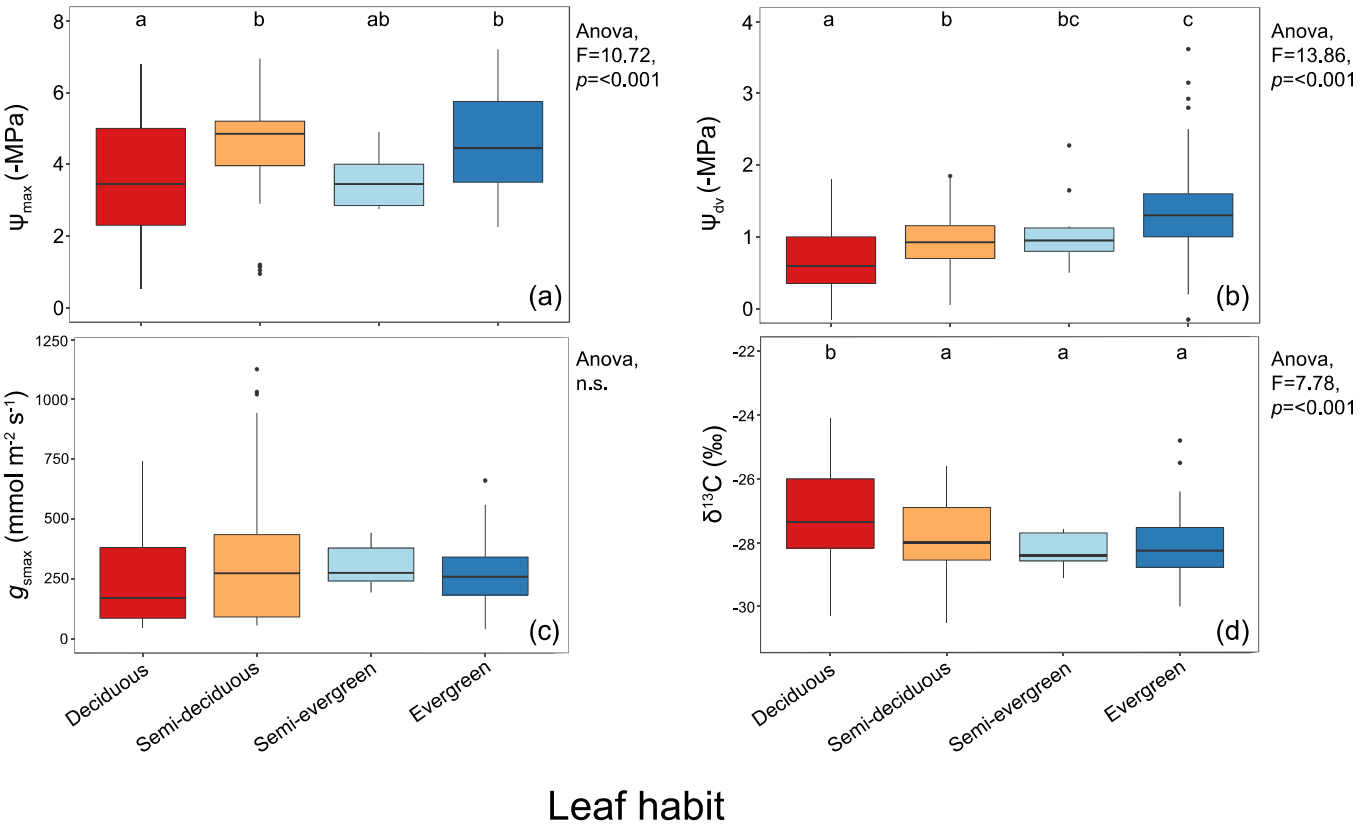

Figure 3.2. Distributions of physiological trait values for 31 TDF species grouped by leaf habit. The center line indicates the median, and the upper and lower box heights indicate the interquartile range. Dots signify outliers. Lowercase letters represent statistical differences according to post-hoc Tukey's mean separation test. Leaf habits that do not share letters are statistically different from one-another.

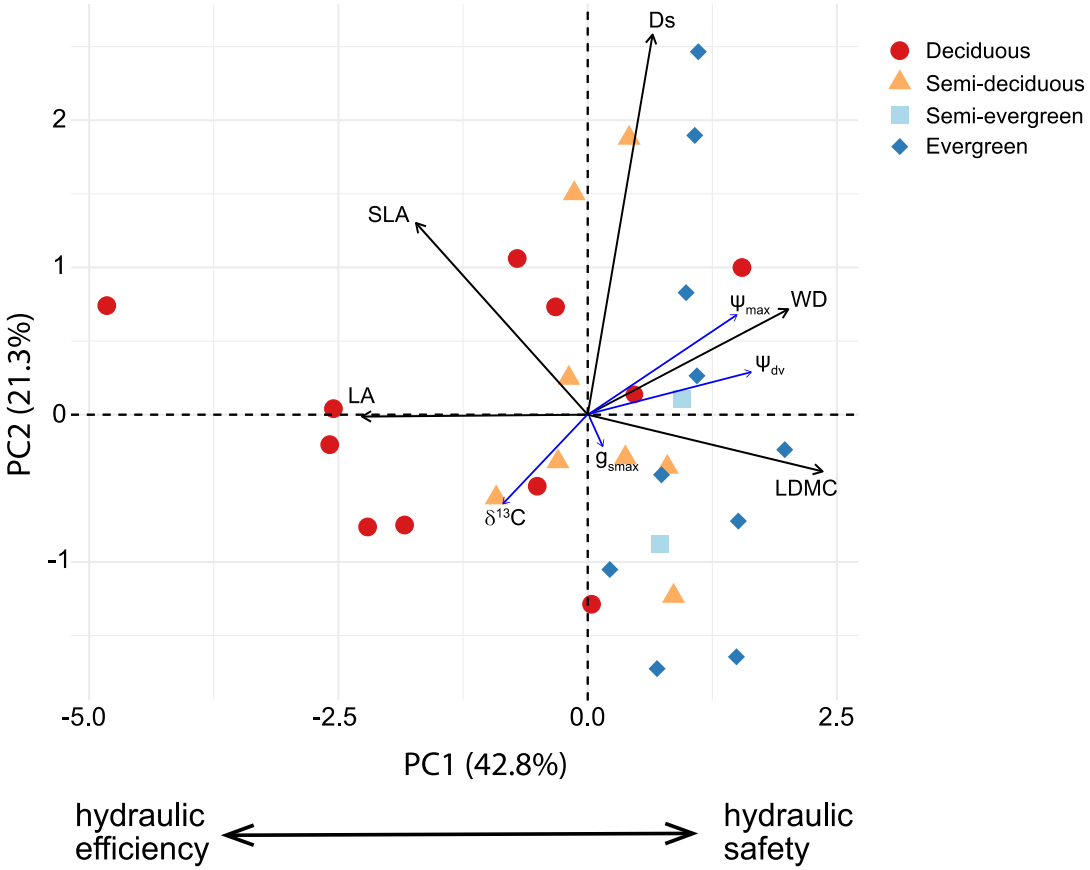

Figure 3.3. Principal component analysis (PCA) biplot showing the first two principal components based upon nine hydraulic traits (five active traits, 4 supplementary traits) for 31 TDF species. The accumulated percentage of explained variance for each axis is indicated in parentheses. Abbreviations found in Table 3.3.

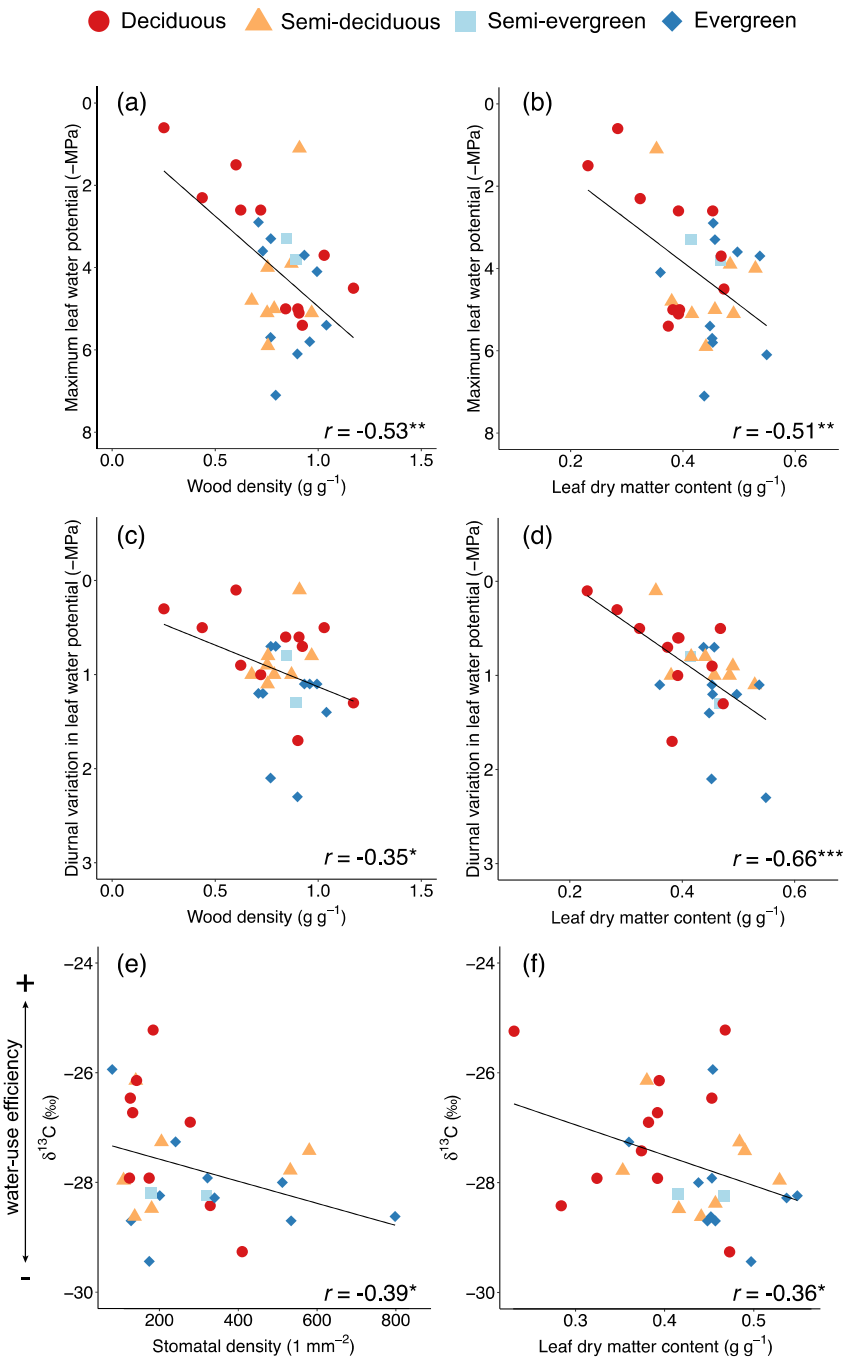

Figure 3.4. Significant relationships between physiological and morphological traits using the mean trait values of 31 TDF species. Regression lines and Pearson's coefficient (*r*) are given. Significance: *, p <0.05; **, p <0.01; ***, p <0.001. δ_{13}C signifies $_{13}$C carbon isotope composition.

CHAPTER FOUR

FUNCTIONAL TRAITS REVEAL LIFE-HISTORY CONSEQUENCES TO RESPROUTING IN CARIBBEAN TROPICAL DRY FOREST.

ABSTRACT

1. Resprouting is of paramount importance in Caribbean tropical dry forest where rates of seedling establishment are low due to strong abiotic constraints. Strong resprouting is thought to come at a cost of lower adult diameter growth as species prioritize allocation to below-ground storage structures. However, in systems where natural disturbances do not result in the loss of above-ground structures, strong resprouting may be associated with fast adult diameter growth as the disturbance regime selects for higher allocation to above-ground organs.

2. We compared 12 traits of 44 Puerto Rican tropical dry forest species to examine relationships among resource strategies, diameter growth and survival adult trees, and resprouting properties pooled from fire, clearcut and hurricane disturbance. We also compared cross-species tests with phylogenetically controlled tests.

3. Resource strategies among species varied along a continuum between resource conservation, leaf and stem investment and drought tolerance vs high potential for resource capture and preference for drought avoidance. Traits were good predictors of adult tree growth which was promoted by cheap investment in leaves and stems, large nutrient rich leaves and lower hydraulic resistance. Survival was not related to variation in resource-use. Resprouting strategies were defined by a resprouting vs drought tolerance trade-off whereby species with fast resource capture strategies (higher leaf nitrogen and phosphorus) grew resprouts quicker but were subject to tighter stomatal control and greater risks from drought (low wood density, high maximum leaf water potential and low diurnal variation in leaf water potential). We found mixed results for

the maintenance of trait x performance and trait x resprouting relationships when controlling for phylogeny, implying some cross-species relationships were not connected to evolutionary history.

4. Resource capture strategies are important to the performance and regeneration of dry forest trees. Contrary to high disturbance severity environments, 'faster' resource use and high allocation to diameter growth result in stronger resprouting responses post-disturbance in this Puerto Rican tropical dry forest.

Key words: Vegetative reproduction, fast-slow, growth, survival, Puerto Rico, trade-offs, functional traits, phylogenetic contrasts.

INTRODUCTION

Disturbance events underpin the dynamics of many terrestrial plant ecosystems, exerting strong evolutionary forces and having consequences for vegetation dynamics, community composition and species coexistence (Clarke *et al.*, 2013; Pausas & Keeley, 2014). In many systems, resprouting represents an important pathway to regeneration, promoting long-term persistence despite constraints imposed by the physical environment or destruction to above-ground biomass (Bellingham & Sparrow, 2000; Bond & Midgley, 2001). This has been well illustrated in drier, less productive ecosystems where low moisture availability inhibits seed germination and resprouting is considered an important component of a plants' life-history (Bond & Midgley, 2001; Clarke *et al.*, 2013). And yet, there may be a cost associated with resprouting in stressful environments if such a strategy is correlated with other life-history trade-offs. Considering the potential implications for species diversity and coexistence, a better understanding is required into the underlying mechanisms driving resprouting in stressful environments.

Species-specific patterns of biomass allocation are considered key to the resprouting behavior trees exhibit. Based upon the well-established storage vs growth trade-off (Bellingham & Sparrow, 2000; Bond & Midgley, 2001; Clarke *et al.*, 2013), resprouting comes at a cost of lower diameter growth rate as trees allocate a greater proportion of their assimilates to storage. Much of this theory has originated from high severity fire environments such as Mediterranean ecosystems where most above-ground biomass is lost and as such many species tend to allocate heavily towards below-ground structures (Bell & Ojeda, 1999; Verdaguer & Ojeda, 2002; Knox & Clarke, 2005). These

plants therefore tend to exhibit lower diameter growth rates but possess greater belowground bud banks and fast resprouting syndromes as recovery is fueled from large storage pools. However, in communities where disturbances are less intense (e.g. in hurricane-prone environments), greater investment in stems may be more advantageous. Under such a scenario, fast diameter growth species may possess the strongest resprouting syndromes as they preferentially allocate towards above-ground organs (Gurvich *et al.*, 2005). Past studies have found mixed support for such patterns of resprouting. Faster growing species on the tropical island of Barro Colorado Island were associated with greater resprouting capacity after a hurricane (Putz *et al.*, 1983; Putz & Brokaw, 1989) but the opposite was found in Puerto Rican tropical wet forest (Zimmerman *et al.*, 1994). Elsewhere, a study from south-east North America determined that there was in fact no link between life-history trade-offs and resprouting ability, rather proposing that resprouting promoted diversity via an alternate trait axis entirely (Dietze & Clark, 2008). Clearly further research is required as to the nature of such a relationship.

In tropical dry forests (TDF) environments, species display a wide range of resource-use behaviors tied to water, tolerance of drought and efficient carbon assimilation (Markesteijn *et al.*, 2011; Medenez-Alonso *et al.*, 2012; Loebeck *et al.*, 2015), and certain studies have suggested a connection with resprouting. For instance, in hurricane-prone regions of the Neotropics both wood density (a proxy for drought resistance) and specific leaf area (investment in leaf area for light capture) were found to be good predictors of resprouting among a small group of species because these traits were associated with tall, fast growing trees that were susceptible to windthrow (Curren

et al., 2008b; Paz *et al.*, 2018). However, these findings are limited in their general applicability across TDFs in part due to the small number of traits and species considered. Determining relationships between resprouting and functional types may be a particular challenge in tropical dry forests where resprouting is widespread and tends to fall along a continuum rather than a dichotomy of responses.

Adopting a mechanistic approach, we assessed the coordination of 12 leaf and stem traits important to the fast-slow trait continuum and general resource economics with tree performance and regeneration in order to better understand life-history consequences of resprouting in Puerto Rican TDF. Within the Caribbean, the structure and composition of forests is determined in large part by the interactive effects of drought and wind (Murphy & Lugo, 1986b; Dunphy *et al.*, 2000; Van Bloem *et al.*, 2007). Species' resprouting capacity varies but is generally widespread among species in response to disturbance and therefore a simple binary categorization (i.e. R+, R-) as previously used in studies from fire-prone systems (Everham & Brokaw, 1996; Vesk & Westoby, 2004) is unlikely to be sufficient. Therefore, we pooled quantitative data regarding resprout initiation and development following three separate disturbance types: hurricanes, clearcutting and fire. Wildfires have no historical role but have become more common in recent decades due to human activity and higher fuel loads linked to invasive African grasses (Brandeis and Woodall, 2008; Thaxton *et al.*, 2012). We asked three main questions: (i) Do TDF species exhibit trade-offs in ecological strategy relating to the fast-slow continuum of resource capture (Reich, 2014)?; (ii) How do traits tied to drought tolerance and the fast-slow continuum scale up to tree performance in terms of

growth and survival?; (iii) Is the interaction between traits and plant performance reflected in the resprouting strategies of dry forest species? We tested the following hypotheses:

- TDF species generally align along an axis of resource capture. On one extreme species tend to possess traits relating to slow tissue turnover, resource conservation and drought tolerance and on the opposite extreme species possess traits conferring fast tissue turnover, high potential for resource capture but lower drought tolerance.
- Stem diameter growth rate is positively related to traits associated with greater carbon gain, more efficient water-use and greater sensitivity to drought conditions but negatively related to tissue construction costs. Survival rate increases with drought tolerance and tissue material strength.
- Species that allocate a greater proportion of resources to storage tend to be better resprouters therefore stronger resprouting will be linked to lower adult tree growth rates but greater survival. Weaker resprouters are predicted to allocate a greater proportion of resources to above-ground growth over roots and therefore will be linked to lower drought tolerance.

MATERIALS AND METHODS

STUDY SITE AND SPECIES

The Guánica tropical dry forest (17°58’ N, 65°30’ W) in SW Puerto Rico was used for this study. On average, the area receives 860 mm of rainfall a year but with considerable interannual variation (Murphy & Lugo, 1986b). The driest period is between December and February however the summer months (May-Aug) are also usually moisture limited. In all, soil moisture deficits typically occur for approximately 10 months of the year. Annual mean potential evapotranspiration exceeds precipitation. The forest exists on a rocky limestone geological formation (karst) that results in relatively alkaline soils and low P bioavailability (Murphy & Lugo, 1986b). Approximately 58% of Guánica is semi-deciduous upland forest and is where this research is focused. Canopy height here is generally 4-7m (4.3m average) and species richness plateaus at around 33 species within 1500m^2 (≥2.5cm dbh). Basal area is 19.8m^2/ ha (stems ≥2.5cm dbh) and is distributed among an average of 12,000 stems/ha (Murphy & Lugo, 1986b). Approximately 42% of the trees are multiple-stemmed (Van Bloem *et al.*, 2003).

In total, we used trait data from 44 of the most dominant tree species, comprising >90% of all individuals ≥2.5cm dbh in the semi-deciduous portion of the forest (Murphy & Lugo, 1986b). Previous research has demonstrated the considerable range among our species in growth form (i.e. number of stems and height; Murphy & Lugo, 1986b; Dunphy *et al.*, 2000) and hydraulic strategies (Allerton & Van Bloem, *submitted*).

TRAIT DATA COLLECTION

We measured 12 leaf and stem traits pertaining to resource economics in tropical dry forest (Table 4.1). Leaf and stem samples were collected from 3-5 individuals per species during the dry season in February 2017 and May-Aug 2017 prior to senescence among deciduous species. Sampling was confined to the outer sun-light canopy of adult trees. When trees were multiple-stemmed, we sampled the largest diameter stem. Standardized protocols were used to sample leaf and stem traits (Cornelissen *et al.* 2003). Mature, undamaged leaves were collected, rehydrated overnight and fresh mass was measured. After using a flatbed scanner to image leaves, the leaf area (LA, cm^2) including the petiole was calculated using the freeware ImageJ (Schneider *et al.* 2012 [https://imagej.net/]). Leaves were then oven-dried at 75°C for 72hr before dry mass was determined. Specific leaf area (SLA, $cm^2\ g^{-1}$) was calculated as surface area/ dry mass and leaf dry matter content (LDMC, $g\ g^{-1}$) as dry mass/ fresh mass. We measured stomatal density (Ds, no. mm^{-2}) by applying clear nail varnish to the abaxial leaf surface, mounting the dry varnish imprints on slides and then counting stomata using a LEXT OLS4000 laser microscope (5X-100X, Kröber *et al.*, 2015). Generally, stomata were counted from 417,315μm^2 surface area but depending on stomata size ranged from 67,340-1,643,520μm^2. Wood density (WD, $g\ cm^{-3}$) was determined with cores extracted with an increment borer (Haglof, Sweden) and fully rehydrated within a vacuum chamber for approximately one week due to their very dense hardwood (many species are $\geq 0.90\ g\ g^{-1}$). Wood volume was measured using the water displacement method, after which samples were oven-dried for 96hr at 100°C and weighed. The WD was calculated as dry

mass/ fresh volume. Corresponding measurements of dry season diurnal (04:00-16:00) stomatal conductance (g_s) and leaf water potential (ψ_l) were made across consecutive days for three leaves per tree in order to capture measurements of g_{smax} and ψ_{max}. In total, five individuals from 31 species were measured using a porometer (SC-1, Decagon Devices) and pressure chamber (Model 1000, PMS Instruments). Logistical constraints prevented us from capturing the g_{smax} and ψ_{max} for all species (Table 4.2). Species-specific water regulation (WR) was also determined as the slope of the dry season relationship between ψ_{max} and $\psi_{predawn}$ (Allerton & Van Bloem, *submitted*). This relationship was proposed by Martinez-Vilalta *et al.* (2014) as a measure of the relative sensitivity of the transpiration rate to declining water availability. Bulk leaf samples from the same five individuals were collected, dried and ground and sent to the Duke DEVIL laboratory for ^{13}C (water-use efficiency, WUE) and N_{mass} determination. ^{13}C was measured to an accuracy of ±0.01% using a Carlo Erba NA 1500 Elemental Analyzer. Additional leaf samples were sent to Clemson's Agricultural Service Laboratory to determine leaf P content (P_{mass}) by using a nitric acid- hydrogen peroxide digestion before ICP-OES analysis (ICP-6500 Duo, Thermo Fisher Scientific, Pittsburg, PA, USA). Gaps in data for SLA and leaf nutrient content were filled from previous dry season research in the forest (Van Bloem, 2004; Allerton, 2013; Sanchez *et al.* 2015) however, not all gaps for all species were able to be addressed (Table 4.2).

GROWTH AND SURVIVAL RATES

Annual tree growth rates (GR, cm yr^{-1}) were obtained from tree dbh measurements in long-term forest plots. Growth rates were based upon slopes produced by regressing the dbh of each tree against corresponding measurement dates. Tree growth rates in Puerto Rican dry forest are relatively low and typically measured in millimeters per year. Therefore, we omitted wet season measurements from analyses as diameter swelling may bias growth rate calculations. Furthermore, if an individual died during our monitoring period, we omitted measurements from the last two censuses prior as trees often stop growing years before eventual death. Care was taken when individuals were added to the dataset to minimize within and between species variation in size in order to account for size-dependent effects on growth. In total, trees were pooled from two proximal sites and growth rates were calculated over a 20.4-26.4 year period between 1992-2019 depending on the site. In total, our analysis included 29 species and the median number of trees per species was 7 (range = 2-138). Only two individuals were available for *Rochefortia acanthophora* and *Plumeria alba*, but all other species had a minimum of 3 individuals. We calculated annual mortality rate using a timespan of 21 years (1998-2019) in order to avoid the potential negative effects of an extended drought period that occurred prior to 1998. Based on Poorter *et al.* (2009), we used the number of trees at the start (N_0) and end (N_1) of the time period and calculated mortality rate as:

$$MR = \frac{log_e\, N_0 - log_e\, N_1}{time\ (yr)}$$

eqn 1

Subsequently, annual survival rate (SR) was calculated as:

$$SR = 100 \times e^{-MR \times 1}$$

eqn 2

RESPROUTING PROPERTIES

We combined resprouting data from plots established post-fire and post-hurricane with historical data collected following clearcutting. Only data on hypogeal sprouting (basal and root suckering) was considered for this study. We attempted to control somewhat for disturbance-specific effects on tree damage by only including data from tree individuals with ≥60% above-ground biomass destruction (quantified observationally). A total of 1015 resprouting individuals were analyzed (704 basal, 311 root). Resprouts from clearcut sites contributed the most individuals to our dataset because above-ground biomass destruction was greatest, but hurricane data contributed the greatest number of resprouting species (Fig. 4.1). Basal resprouts included any woody twig growing at the base of a tree no more than 30cm up mature stems and at an angle <45° (Dunphy, 1996; Van Bloem *et al.*, 2003). Measurements on resprout initiation and development were made by first, taking an inventory of all new sprouts on individuals after 101-133 days depending on the site (119 days on average) and secondly, measuring the length of the longest resprout to the nearest cm. Measurements from all disturbances were then pooled and a species-specific median RS_{num} and RS_{len} was calculated. The resprout relative height growth rate (RS_{RGR}) was calculated using an initial true mean height (H_1) of 0.1cm and the equation:

$$RS_{\mathrm{RGR}} = \frac{(\overline{\ln H_2} - \overline{\ln H_1})}{(t_2 - t_1)}$$

eqn 3

We ln-transformed the heights before averaging rather than averaging first, a method shown to help negate bias associated with increases in RGR variance with higher sample sizes (Hoffmann & Poorter, 2002). Resprout capacity (RS_{cap}, unitless) is defined as the relative ability of a plant species to initiate new shoots using reserves after disturbance has caused significant above-ground biomass destruction (AGBD; Cornelissen *et al.*, 2003). The RS_{cap} method is seen as a compromise between rapid assessment and precision of determining interspecific differences in post-disturbance recovery (Cornelissen *et al.*, 2003). Only fire and hurricane data were included in the calculation of RS_{cap} as historical clearcut data did not include individuals that failed to resprout. All individuals (n = 535, within species range n = 3-107, median n =10) determined to have lost ≥60% above-ground biomass were included in the RS_{cap} equation:

$$RS_{\mathrm{cap}} = \frac{AGBD_{ind} \cdot RS_{pop}}{100}$$

eqn 4

where $AGBD_{ind}$ is the average percentage of AGBD among individuals, and RS_{pop} is the percentage of the population that resprouted. RS_{cap} ranges from 0-100 (unitless), where 100 represents all individuals within a species resprouting, despite high AGBD.

STATISTICAL ANALYSES

We assessed normality of trait data with visual assessment of distributions and Shapiro-Wilks tests and log transformed data when necessary. To determine axes of trait variation among our 44 tree species, we used the mean species values for 12 leaf and stem traits and analyzed multivariate trait associations using a principal-component analysis (PCA). For the purposes of our PCA only, gaps in our database were addressed by imputing trait values based upon the closest sister species from our phylogenetic tree (see Table 4.2 for details on missing data and Fig. 4.2 for phylogenetic tree). After confirmation of the most significant traits along each principal component (Table 4.3 for loadings), we decided to omit Ds from subsequent analysis based on its insignificant role in strategy variation. Species-specific performance and resprouting values were not included in this initial analysis but plotted *a posteriori* against the PCA axes (Table 4.4). Species-level loadings were extracted in order to observe how species were situated in respect to multivariate trait space (Table 4.5). Using mean species values, relationships between leaf and stem traits with tree performance (GR and SR) and resprouting (RS_{num}, RS_{len}, RS_{RGR} and RS_{cap}) were determined using Pearson's pairwise correlations and phylogenetic correlations. The choice of Pearson's correlation (rather than regression) allowed us to directly compare the signs and strengths of cross-species and phylogenetic correlations (Poorter *et al.*, 2009). For correlation tests, species that were determined to have a mean resprout number of zero (i.e. did not resprout) were omitted from analyses because we sought to link functional responses directly to resprout development. Five species showed no evidence of resprouting including *Elaeodendrum xylocarpum*, *Erythroxylum areolatum*, *Helicteres jamaicensis*, *Plumeria alba* and *Zanthoxylum flavum*. We used Felsenstein's

(1985) phylogenetic independent contrasts (PIC) method to determine whether cross-species relationships were consistent from an evolutionary point of view. A phylogenetic tree was constructed using the 'brranching' package in R (Chamberlain, 2020) based upon a well-resolved angiosperm phylogeny (tree R20120829) by Smith *et al.* (2011) (Fig. 4.2). We used an unbiased approach to resolving the one polytomy in our tree by placing a new node at zero distance from the original polytomous node. Phylogenetic independent contrasts (PICs) for traits were calculated using the 'ape' package (Paradis & Schliep, 2018). Before conducting correlations with PICs, we confirmed model assumptions including whether PICs conformed to a half normal distribution, whether branch lengths were arbitrarily large and if observed variation in traits was predicted by the phylogeny structure under a Brownian motion model of trait evolution (Freckleton, 2001). As PICs must have a mean of zero, correlation analyses were calculated through the origin (Garland, 1992). All analyses were conducted in R.3.5.2 (R Development Core Team, 2019).

RESULTS

ASSOCIATION AMONG TRAITS

The first principal component (PC) of our principal component analysis explained 30% of the total variation and represents the fast-slow trait continuum as it pertains to tropical dry forests and the trade-off between growth vs. persistence (Fig. 4.3a). The positive side of the axis reflects resource acquisitive species (Fig. 4.3b, Table 4.3) with high wet

season carbon gain and high growth rates. These species were generally deciduous or semi-deciduous (Fig. 4.3b) and therefore considered drought 'avoiders' as they possess greater stomatal sensitivity to soil drought (lower WR) and low g_{smax} in the dry season. Acquisitive strategies are characterized by high SLA, P_{mass}, N_{mass}, LA and higher water-use efficiency (lower $\delta_{13}C$ discrimination) (Fig. 4.3a). The negative side of the axis indicates slower growth, drought tolerant (more negative ψ_{max}, greater ψ_{dv}) species that allocate a greater proportion of their resources to structural resistance (higher LDMC and WD). These species are generally able to maintain moderate gas-exchange in the dry season (higher g_{smax}). There was also a weak correlation between the length of longest resprout (RS_{len}) and PC1 (Table 4.4). In total, PC2 explained 18% of the trait variation and was characterized by drought tolerant species (more negative ψ_{max} and high WD) with higher WR (a $\psi_{predawn}$ x ψ_{midday} slope closer to 1) that possessed more acquisitive leaf traits (higher N_{mass}, P_{mass} and SLA). These species encompassed all leaf habit types (Fig. 4.3b) and also tended to produce more resprouts (higher RS_{num}) (Table 4.4). Five PCs were necessary to explain 75% of the variation among traits (Table 4.3).

Cross-species correlations between leaf and stem traits also conformed to the expected trade-offs between fast and slow strategies (Table 4.6). These included negative relationships between SLA and LDMC (r_c = -0.35, p<0.01), P_{mass} and WD (r_c = -0.35, p<0.05), LA and ψ_{max} (r_c = -0.56, p<0.01) and WUE and N_{mass} (r_c = -0.37, p<0.05).

RELATIONSHIPS BETWEEN TRAITS AND PERFORMANCE

Growth rate was positively correlated with SLA, LA and P_{mass} of the species (Fig. 4.4, Table 4.6) and negatively correlated to LDMC, WD and ψ_{max} (Fig 4.4., Table 4.6). Therefore, species with faster growth rates were linked to greater resource acquisition strategies but tended to be less drought tolerant, investing less in tissue structures. Growth rate correlated best with wood density (r_c = -0.60, p<0.001) and P_{mass} (r_c = 0.50, p<0.01). Surprisingly, survival rate was not found to be correlated with any of our leaf and stem traits (Table 4.6).

Qualitatively, phylogenetically-independent correlations (r_p) were found to be similar to cross-species (r_c) results, although in some cases the strength of relationships changed (Fig. 4.4, Table 4.6). Interestingly, the phylogenetic (r_p) correlation between N_{mass} and GR was significantly positive whereas the cross-species correlation was not (r_c = 0.36_{ns} vs r_p = 0.46, p<0.01). Similarly, survival rate was positively associated with WR (i.e. higher survival among species with a lower degree of stomatal sensitivity) in the phylogenetic (r_p) analysis but not in the cross-species (r_c) one (r_c = 0.28_{ns} vs. r_p = 0.40, p<0.05).

IS RESPROUTING RELATED TO TRAITS AND PERFORMANCE?

Both the median length of longest resprout and resprout RGR was higher among species with faster adult growth rates (Fig. 4.4). Resource acquisitive traits also scaled with resprouting, as species with higher P_{mass} were found to both produce a greater number of resprouts and grow them faster (Fig. 4.5, Table 4.6). Higher rates of resprout growth were also linked to leaves with higher N_{mass} and LA as well as lower WD, ψ_{dv} and dry season

g_{smax} (Fig. 4.5, Table 4.6). The capacity of species to resprout post-disturbance (RS_{cap}) was not found to be correlated with any of our trait or performance variables (Table 4.6).

A number of traits maintained similar relationships in direction and strength with resprouting properties under phylogenetically-independent (r_p) analysis including P_{mass} vs RS_{num}, N_{mass} vs RS_{len} and WD vs RS_{RGR}. (Fig. 4.5, Table 4.6). Both LA and g_{smax} remained positively associated with RS_{RGR} with the phylogenetically-independent correlation much stronger (Fig. 4.5, Table 4.6). Interestingly, GR and P_{mass} did not maintain positive relationships with RS_{len} or RS_{RGR} when controlling for species' shared history (Fig. 4.4 & 4.5, Table 4.6). Similarly, cross-species (r_c) correlations of g_{smax}, ψ_{dv} and LA vs RS_{len} were no longer significant when accounting for species' shared history (Fig 4.5, Table 4.6). In six cases, the phylogenetically-independent (r_p) correlations were significant but the cross-species (r_c) correlations were not including for SLA and WUE vs RS_{RGR} (Fig. 4.5, Table 4.6), and N_{mass}, ψ_{dv}, ψ_{max} and SR vs RS_{num} (Table 4.6).

DISCUSSION

PUERTO RICAN TROPICAL DRY FOREST SPECIES ALIGN WITH A FAST-SLOW CONTINUUM IN RESOURCE CAPTURE

Analysis of multivariate trait space among 44 TDF species revealed distinct trade-offs relating to resource acquisition vs conservation and drought avoidance vs drought tolerance. Based on our PCA, one extreme of PC1 reflects species with well protected

leaves and stems (with high initial construction cost) that help negate the negative effects drought stress and moderate dry season gas exchange have on leaf turgor and xylem hydraulic conductivity. The other extreme along this axis is occupied by species with 'cheaper' leaves and stems that maximize assimilation during wetter periods but must tightly control dry season gas-exchange to prevent hydraulic failure driven by excessive transpiration. This trade-off axis represents the coordinated ways traits vary in TDF to determine water economics and is well described in other Neotropical dry forests including southern Mexico and eastern Bolivia (Lohbeck *et al.*, 2015; Markesteijn *et al.*, 2011). The second PC axis characterized more intermediate resource strategies whereby species were able to combine moderate drought tolerance with faster rates of resource capture thus highlighted the variability of trait combinations that exist in dry forest. A number of deciduous and semi-deciduous species are well characterized by intermediate resource strategies (Fig. 4.3b), presumably utilizing their greater stem resistance to prolong photosynthesis later into the dry season before leaf abscission.

RESOURCE ECONOMICS IS STRONGLY TIED TO PERFORMANCE

We hypothesized that stem diameter growth rate would be positively associated with traits pertaining to higher C gain, more efficient water-use and greater sensitivity to drought but negatively to investment in tissue structures. Overall, our leaf and stem traits were good predictors of plant performance and provided strong evidence for our hypothesis. Species with lower drought tolerance (less negative ψ_{max}, lower WD and LDMC) were characterized by higher growth rates (Fig. 4.4) and possessed leaf traits that

facilitated fast growth including higher SLA and P_{mass}. High SLA facilitates higher assimilation rates per unit leaf area (Niinemets, 1999; Reich *et al.*, 1997) and higher P_{mass} is an indication of more efficient photosynthetic machinery, both implying quicker returns on investment in the form of tree growth (Wright, 2004). Similarly, leaf attributes fundamental to fast C gain including SLA, leaf N content, A_{mass} and chlorophyll content have been shown to be important in determining adult tree growth rates in both the dry (Chaturvedi *et al.*, 2011) and wet tropics (Poorter & Bongers, 2006). It is likely higher concentrations of leaf P are especially relevant to rates of above-ground net primary productivity in this P-limited system and may suggest faster growing species possess higher rates of nutrient resorption prior to senescence (Lugo & Murphy, 1986, Niklas *et al.*, 2005) or specific mycorrhizal associations that enhance P uptake (Moyersoen *et al.*, 1998; Plassard & Dell, 2010). Faster growth, high SLA species with nutrient-rich leaves also tended to favor deciduous patterns of phenology (Fig. 4.3) illustrating a possible trade-off between high resource acquisition and shorter leaf life span and slow resource acquisition and longer leaf life span (Sobrado, 1991; Hulshoff *et al.*, 2013). However, the strength of this trade-off likely weakens in communities containing significant proportions of intermediate leaf habit species characterized by a broader group of trait combinations such as in TDFs (Allerton & Van Bloem, *submitted*, Powers & Tiffin, 2010, Brodribb & Holbrook, 2004).

Drought tolerance in a key persistence trait in TDF that enables species to withstand prolonged periods of drought, but the trade-off is a markedly lower growth rate as illustrated by our findings. As predicted, ψ_{max} and WD were negatively correlated with

growth in our cross-species analyses (Fig. 4.4) because these traits vary inversely with leaf and sapwood-specific hydraulic conductance (Santiago *et al.*, 2004; Markesteijn *et al.*, 2011a). The lower water transport efficiency modulates gas-exchange and photosynthesis and ultimately results in low GR (Chave *et al.*, 2009; Wright *et al.*, 2010; Poorter *et al.*, 2010). The tight association between hydraulics and assimilation has been well documented in other Neotropical forests (Brodribb *et al.*, 2002; Santiago *et al.*, 2004). We found no clear trend of dry season g_{smax} with GR (Fig. 4.4) which may be best explained by differences between fast and slow growing species in their allocation of assimilated carbon to growth vs respiration (slower growers generally have higher respiration requirements) (Poorter *et al.*, 1990).

We hypothesized that survival would increase with greater drought tolerance and tissue material strength, however surprisingly we detected no such relationship (Table 4.6). Meta-analytical studies encompassing data from forest biomes across the globe have successfully tied a number of physiological and morphological hydraulic traits including hydraulic safety margins, xylem vulnerability to embolism and wood density to drought-induced mortality (Anderegg *et al.*, 2016; O'Brien *et al.*, 2017). The high rates of clonality, low root:shoot ratios and conservative resource economics in our forest are indications that species generally converge towards a strategy of long-term persistence vs growth (Lambers & Poorter, 1992; Wright *et al.*, 2010) and therefore the timespan (21 years) over which we calculated survival may have been insufficient to detect trends.

Ultimately however, our data represent indirect evidence for the growth vs survival trade-off as slow-growing species prioritize investment in LDMC and WD to maximize

cavitation resistance during drought stress through smaller vessel diameters and greater vessel density (Poorter & Bongers, 2009; Markesteijn *et al.*, 2011b). Although the risk of drought-induced death is higher among fast growers with low-density tissue (Chave *et al.*, 2009; O'Brien *et al.*, 2017), many of these species possess alternative drought adaptation mechanisms including isohydricy, deciduousness, stem water storage, and soil water access (Lugo *et al.*, 1978; Medina & Cuevas, 1991; Wolfe & Kursar, 2015; Allerton & Van Bloem, *Chapter 3*). Cross-species correlations remained significant when accounting for phylogenetic relatedness, and in certain cases were much stronger in strength. The results of our analysis therefore indicate that measured growth and trait variables may be part of the same adaptive network, and not simply down to coevolution within closely related taxa.

VARIATION IN RESOURCE CAPTURE AND ADULT GROWTH AFFECT POST-DISTURBANCE RECOVERY

Species that were stronger resprouters were hypothesized to have lower growth rates as they allocate a high proportion of captured resources to non-structural carbohydrate stores that fund regrowth. Further, weaker resprouters were predicted to allocate a greater proportion of resources to above-ground growth vs roots and therefore would be less drought tolerant. We found evidence of differences in leaf traits and water-use between co-existing species with contrasting resprouting patterns, however contrary to expectations, stronger resprouters (i.e. higher RS_{len} and RS_{RGR}) were associated with higher adult tree growth rates and possessed fast traits (e.g. high LA, N_{mass} and P_{mass}) that

fueled growth (Fig. 4.4 & 4.5). Lower WD, ψ_{dv} and dry season g_{smax} among strong resprouting species also suggested a lower degree of drought tolerance, controlled for via tight leaf level adjustment of stomata during periods of low soil water availability (Fig. 4.5). Various components of fast trait syndromes have been found among resprouting woody species in fire-adapted sub-dry and chaparral Mediterranean environments including lower LMA (inverse of SLA), higher N_{area} and lower drought resistance linked to a lack of sclerophyllous leaves (Paula & Pausas, 2006; Ackerly, 2004) however, in some cases the opposite was true (cf. Vilagrosa *et al.*, 2014). An observation often made among Mediterranean plants is that drought resistance is not synonymously linked to root mass (Paula & Pausas, 2006; Schwilk & Ackerly, 2005). Interestingly, within Mediterranean systems, resprouters have been observed to have deep root systems but relatively low drought tolerance (Saura-Mas & Lloret, 2007; Pratt *et al.*, 2007). By contrast, high drought resistance has been used to infer extensive root systems within our TDF where the proportion of root:total biomass is particularly high (~50%; Murphy & Lugo, 1986b).

These findings represent how the dynamic interaction between the environment and disturbance strongly influence patterns of resprouting. From a disturbance perspective, stronger resprouting among fast growth species is in agreement with the theory that spatial allocation patterns among resprouting species may be different in areas of lower disturbance severity as investment in above-ground structures has greater value (Bellingham & Sparrow, 2000). Alternatively, fast-growth species may not require high allocation to storage as strong initial resprouting enables species to quickly begin

subsidizing recovery via new assimilates (Bond & Midgley, 2001). However, from the perspective of persisting through drought these results demonstrate the trade-off between resprout growth and drought tolerance. Conservative, drought tolerant species with slow resprouting may still allocate heavily to belowground structures (e.g. to maximize access to groundwater). However, height growth may be offset by a greater investment of internal C towards resprout tissue structures (i.e. higher WD & LDMC) that increase hydraulic resistance and survival during drought periods. This does not account however for ontogenetic-related differences in traits. The relationship between resprouting, adult performance and resource-use likely has implications for demographic processes over space and time as the balance between fast trait species dominance and slow trait species persistence shifts depending on the relative frequency of high vs low intensity disturbance. The convergence of most dominant species though towards drought tolerant strategies (Allerton & Van Bloem, *submitted*) is in agreement with low water availability being the main influence on forest structure (Dunphy *et al.*, 2000). These trade-offs may also translate into temporal constraints on resprouting depending on the time of year disturbance occurs (e.g. fires during the dry season may favor resprouting among drought tolerant species) (Paula & Pausas, 2006). Our PCA appears to show some alignment of fast traits and resprout growth with deciduousness (Fig. 4.3b) suggesting that for these species the use of alternative mechanisms to withstand drought likely contribute towards their resprouting success – primarily drought avoidance through leaf drop but also photosynthetic stems (as in the case of *B. simaruba*) as well as compound leaves (Aschan & Ptanz, 2003; Yates *et al.*, 2010).

Relationships between resprouting, traits and growth were less consistent when accounting for evolutionary-independence as a number of r_p correlations were weak or non-significant (Fig. 4.4 & 4.5). Ultimately, based on our selected species, strong resprouting and adult growth appear to be confined to a subset of clades within our larger evolutionary tree. Interestingly, many of the species within these clades are associated with unique traits that may set them apart in their strong growth and resprouting including the ability to fix nitrogen (Fabaceae *sp.*), photosynthetic stems (*B. simaruba*) and ectomycorrhizal fungi (Polygonaceae and Nyctaginaceae *sp.*). Further investigation is needed into whether this relationship extends beyond the subset of families we have identified here.

CONCLUSION

Our study demonstrates that traits characterizing the resource-use strategies of TDF species are good predictors of growth and resprouting, and that resprouting patterns are driven by the dynamic interaction between the environment and disturbance.

In effect, low-intensity disturbance in our tropical dry forest selects for above-ground allocation, fast growth rates and strong resprouting, however only when species possess the necessary drought avoidant mechanisms. At the same time, most species trade-off strong resprouting for drought tolerance illustrating the dominant role of water-availability in recovery dynamics. The implications of these life-history strategies for long-term persistence go beyond the scope of this study. Rather than framing these findings in terms of winners vs losers, the tortoise and the hare analogy (Bond, 1989)

seems more appropriate whereby TDF recovery dynamics may be characterized in part by the shifting balance of fast-trait species dominance and slow-trait species persistence. Ultimately their relative contributions within recovering sites will likely differ depending the type, intensity and frequency of disturbance and its effect on local resource dynamics.

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TABLES

Table 4.1. List of functional traits pertaining to resource economics, performance and regeneration used in this study.

Abbreviation	Trait	Units
Resource economics		
SLA	Specific leaf area	$cm^2\ g^{-1}$
LDMC	Leaf dry matter content	$g\ g^{-1}$
LA	Leaf area	cm^2
N_{mass}	Leaf nitrogen content	%
P_{mass}	Leaf phosphorus content	$mg\ g^{-1}$
WD	Wood density	$g\ cm^3$
ψ_{max}	Dry season maximum leaf water potential	-MPa
ψ_{dv}	Dry season diurnal variation in leaf water potential	-MPa
WR	Dry season ψ_{midday} x $\psi_{predawn}$ regression slope	unitless
g_{smax}	Dry season maximum stomatal conductance	$mmol\ m^{-2}\ s^{-1}$
Ds	Stomatal density	$no.\ mm^{-2}$
WUE	^{13}C isotope discrimination	‰
Performance		
GR	Adult tree growth rate	$cm\ yr^{-1}$
SR	Adult tree survival rate	$\%\ yr^{-1}$
Regeneration		
RS_{num}	Number of resprouts	number of sprouts in first 119 days
RS_{len}	Length of longest resprout	length attained in first 119 days
RS_{RGR}	Resprout relative growth rate	$cm\ cm^{-1}\ day^{-1}$
RS_{cap}	Species-specific resprouting capacity	unitless

TABLE

Table 4.2. Traits and the species for which data was missing from our analyses. For the PCA, missing values were imputed using trait data from the closest sister species in our phylogenetic tree (Fig. 4.2).

Traits	SLA, LDMC and LA	P_{mass} and WD (n = 1)	N_{mass} (n = 8)	ψ_{max}, ψ_{dv}, WR, WUE, Ds, g_{smax} (n = 13)
Missing species	None	*Rochefortia acanthophora*	*Coccoloba krugii* *Croton discolor* *Croton glabellus* *Lantana involucrata* *Reynosia uncinata* *Rochefortia acanthophora* *Stenostomum acutatum* *Wedelia calycina*	*Coccoloba krugii* *Colubrina elliptica* *Croton discolor* *Croton glabellus* *Helicteres jamaicensis* *Lantana involucrata* *Reynosia uncinata* *Rochefortia acanthophora* *Samyda dodecandra* *Savia sessiliflora* *Stenostomum acutatum* *Swietenia mahoganii* *Wedelia calycina*

Table 4.3. Trait loadings for 'active' variables in our principal component analysis including leaf and stem traits pertaining to the fast-slow economic spectrum in dry forest species. Where indicated, traits were log transformed to improve analysis. Proportion of variance explained by each principal component (PC) is recorded in parentheses. Functional traits include: specific leaf area (SLA), lead dry matter content (LDMC), leaf nitrogen content (N_{mass}), leaf phosphorus content (P_{mass}), dry season maximum leaf water potential (ψ_{max}), dry season diurnal variation in leaf water potential (ψ_{dv}), leaf area (LA), regression slope of dry season relationship between $\psi_{predawn}$ vs ψ_{midday} (WR), wood density (WD), carbon isotope composition (WUE), stomatal density (Ds), dry season maximum stomatal conductance (g_{smax}).

Trait	PC1 (0.30)	PC2 (0.18)	PC3 (0.12)	PC4 (0.08)	PC5 (0.07)
SLA	0.66	0.47	-0.02	0.12	-0.32
LDMC	-0.65	0.09	0.06	-0.35	0.45
LA (log)	0.79	0.12	-0.04	-0.15	0.32
N_{mass}	0.63	0.54	0.24	-0.01	0.08
P_{mass}	0.71	0.36	0.04	0.15	0.17
ψ_{max}	-0.54	0.63	-0.04	0.12	-0.44
ψ_{dv}	-0.67	0.31	0.03	0.22	-0.01
WR (log)	-0.15	0.70	0.45	-0.14	0.17
WD (log)	-0.49	0.47	0.20	-0.30	-0.01
WUE (log)	0.28	-0.30	0.75	0.01	-0.10
Ds	-0.03	0.41	-0.61	0.30	0.32
g_{smax}	-0.35	-0.12	0.46	0.68	0.30

Trait 4.4. Correlation of supplementary variables pertaining to tree performance and resprouting to each principal component from the analysis of leaf and stem functional traits. Proportion of variance explained by each principal component (PC) is recorded in parentheses. Abbreviations include: adult tree growth rate (GR), adult tree survival rate (SR), number of resprouts (RS_{num}), length of longest resprout (RS_{len}), resprout relative growth rate (RS_{RGR}), species-specific resprout capacity (RS_{cap}).

Performance and resprouting	PC1 (0.30)	PC2 (0.18)	PC3 (0.12)	PC4 (0.08)	PC5 (0.07)
GR	0.60	-0.14	-0.04	0.19	0.15
SR	0.15	0.24	0.26	-0.18	-0.07
RS_{num}	0.01	0.37	0.08	0.10	-0.13
RS_{len}	0.25	0.13	-0.15	-0.18	0.08
RS_{RGR}	-0.10	0.09	-0.04	-0.02	-0.07
RS_{cap}	-0.20	0.04	-0.12	0.11	-0.10

Table 4.5. Species level loadings for the principal component analysis of 12 leaf and stem traits pertaining to the fast-slow economic spectrum among 44 Puerto Rican dry tropical forest. Total species $n = 44$. Proportion of variance of each principal component (PC) is recorded in parentheses.

Species	PC1 (0.30)	PC2 (0.18)	PC3 (0.12)	PC4 (0.08)	PC5 (0.07)
Amyris elemifera L.	-1.33	2.51	0.48	0.52	1.11
Bourreria succulenta Raf.	0.05	-0.38	1.66	0.56	-0.82
Bucida buceras (L.)	-0.75	0.14	0.59	0.04	0.31
Bursera simaruba (L.) Sarg.	5.31	-2.04	-3.25	0.85	-0.24
Coccoloba diversifolia Jacq.	0.04	-1.92	-2.09	-1.93	-0.78
Coccoloba krugii Lindau	-0.47	0.06	0.15	-1.68	-0.44
Coccoloba microstachya Willd.	-1.00	-0.39	-0.08	-1.89	-0.29
Colubrina arborescens (Mill.) Sarg.	1.15	1.15	0.97	-0.58	-0.11
Colubrina elliptica (Sw.) Brizicky & W.L. Stern	1.82	1.73	0.94	0.11	-1.40
Comocladia dodonea (L.) Urb.	1.93	-1.24	-1.45	0.48	1.22
Crossopetalum rhacoma Crantz	-1.34	-1.25	-0.41	-0.35	-0.44
Croton discolor Willd.	-0.51	0.36	-0.72	0.42	-0.94
Croton glabellus L.	0.09	0.96	-0.75	0.22	-0.83
Elaeodendrum xylocarpum (Vent.) DC.	-2.84	-1.98	-1.63	-0.35	0.16
Erithalis fruticosa L.	-1.84	-1.48	-0.31	-0.09	-0.61
Erythroxylum areolatum L.	1.42	2.01	-0.16	-0.77	-1.21
Erythroxylum rotundifolium Lunan	0.01	0.98	-0.71	-1.47	-1.02
Eugenia foetida Pers.	-2.44	1.62	-1.34	2.13	0.67
Eugenia rhombea Krug & Urb.	-2.34	-0.13	-1.28	0.65	-0.58
Exostema caribaeum (Jacq.) Roem. & Schult.	-0.17	1.89	1.08	1.17	-0.33
Guettarda elliptica Sw.	-1.10	0.33	0.50	1.16	-0.55
Guettarda krugii Urb.	-1.31	0.18	0.11	1.11	0.98
Gymnanthes lucida Sw.	-0.79	1.10	-0.57	-0.07	-0.16
Helicteres jamaicensis Jacq.	3.25	-0.42	-1.40	0.53	1.33
Jacquinia berteroi Spreng.	-1.90	-3.70	0.97	0.19	-1.30
Krugiodendron ferreum (Vahl) Urb.	-1.13	1.91	-1.09	0.62	0.19
Lantana involucrata L.	-0.53	-0.74	1.44	0.89	-1.22
Leucaena leucocephala (Lam.) de Wit	1.64	0.92	1.08	0.88	1.11
Mosiera xerophytica (Britton) Salywon.	-1.89	-0.27	-0.63	0.23	0.65
Pictetia aculeata (Vahl) Urb.	1.00	0.47	2.68	0.06	0.65
Pisonia albida (Heimerl) Britton	3.05	-0.47	0.50	1.31	0.27
Pithecellobium unguis-cati (L.) Mart.	0.88	2.07	-0.76	-0.31	0.31
Plumeria alba (L.)	4.10	-1.71	0.40	0.31	0.08
Reynosia uncinata Urb.	-2.66	-1.01	-0.59	0.36	1.60
Reynosia vivesiana Trejo	-2.12	-0.64	-0.69	0.02	1.43
Rochefortia acanthophora (DC.) Griseb.	-3.43	-0.79	2.09	-0.78	0.38
Savia sessiliflora (Sw.) Willd.	1.03	1.85	-0.28	-1.23	-0.39
Samyda dodecandra Jacq.	1.65	2.40	0.14	-1.12	-0.79
Stenostomum acutatum DC.	0.00	-0.28	-0.11	1.01	-1.23
Swietenia mahoganii L.	0.90	-2.00	1.28	-1.61	1.93
Tabebuia heterophylla (DC.) Britton	0.08	-1.00	1.65	0.08	0.54
Thouinia portoricensis Radlk.	-1.09	2.07	-1.36	-1.35	0.77
Wedelia calycina Rich.	0.86	-2.23	1.14	0.91	-1.73
Zanthoxylum flavum Vahl	2.72	-0.64	1.80	-1.21	1.70

Table 4.6. Pairwise Pearson's correlations between leaf, stem, performance and regeneration traits. Standard cross-species comparisons (r_c) are below the diagonal (species n = 30-44) and phylogenetic correlations (r_p) based on independent contrasts are below the diagonal (species n = 25-44). Coefficients in bold indicate significant relationships. * p = <0.05, ** p = <0.01, *** p = <0.001. [1]log transformed before analysis.

Trait	SLA	LDMC	LA[1]	N_{mass}	P_{mass}	WD[1]	ψ_{max}	ψ_{dv}	WR[1]	$g_{smax\ 1}$	WUE [1]	GR	SR	RS_{num}	RS_{len}	RS_{RGR}	RS_{cap}
Resource economics																	
SLA		**-0.41****	**0.56*****	**0.62*****	**0.48****	**-0.40****	0.08	-0.17	**0.45***	-0.34	-0.13	**0.60*****	0.15	0.20	0.19	**0.44***	0.06
LDMC	**-0.35****		**-0.44****	**-0.35***	-0.18	0.25	0.33	0.56	-0.03	0.31	0.12	**-0.70*****	0.14	-0.12	-0.23	-0.25	**-0.40***
LA	**0.46*****	**-0.46****		0.16	0.17	**-0.69*****	**-0.52****	-0.35	0.21	-0.08	0.02	**0.61*****	0.18	-0.27	-0.20	**0.39***	-0.12
N_{mass}	**0.65*****	-0.35	**0.56*****		**0.58*****	-0.05	**0.45***	0.03	0.36	-0.10	**-0.42***	**0.46****	0.08	**0.72*****	**0.43***	-0.09	0.27
P_{mass}	**0.48****	-0.34	**0.55*****	**0.74*****		-0.31	0.18	0.17	0.17	-0.03	-0.32	**0.55****	0.03	**0.45***	0.06	0.14	-0.31
WD[1]	-0.29	**0.51***	-0.27	-0.11	**-0.35***		**0.42***	0.10	-0.01	0.13	-0.01	**0.52****	-0.35	0.26	0.15	**-0.48***	**0.54****
ψ_{max}	0.03	**0.50****	**-0.56****	-0.21	-0.28	**0.46****		**0.57*****	**0.45***	-0.10	-0.10	**-0.40***	0.07	**0.50***	0.07	-0.29	0.02
ψ_{dv}	-0.22	**0.59*****	**-0.45****	-0.17	-0.13	0.37	**0.57*****		0.30	0.18	0.21	-0.23	0.08	**0.44***	-0.36	-0.28	-0.24
WR[1]	0.31	0.27	0.11	**0.42***	0.12	**0.36***	**0.41***	**0.37***		-0.11	0.03	-0.08	**0.40***	0.13	-0.13	0.26	-0.06
g_{smax1}	-0.15	0.16	-0.20	-0.06	-0.19	0.17	0.17	0.24	0.31		-0.24	0.09	0.33	0.01	-0.31	**-0.63*****	-0.06
WUE[1]	-0.05	**0.35***	-0.20	**-0.37***	-0.18	0.06	0.33	0.32	-0.01	-0.14		-0.07	-0.24	0.17	0.21	**0.48***	0.35
Performance																	
GR	**0.47****	**-0.42***	**0.41****	0.36	**0.50****	**-0.60*****	**-0.43***	-0.35	-0.13	-0.03	0.05		-0.02	0.34	0.06	0.13	0.15
SR	0.28	0.07	0.02	0.32	0.17	-0.02	0.12	0.05	0.28	0.05	-0.09	-0.02		**0.52****	0.13	-0.01	0.14
Regeneration																	
RS_{num}	0.09	-0.08	-0.06	0.31	**0.39***	0.00	0.10	0.15	0.21	0.00	0.26	0.37	0.12		0.27	-0.25	**0.49***
RS_{len}	0.40	-0.16	**0.42****	**0.47***	**0.46****	-0.37	-0.32	**-0.42***	-0.02	**-0.43***	0.12	**0.49****	-0.01	0.19		0.26	**0.52****
RS_{RGR}	0.24	-0.03	**0.20***	0.23	**0.53****	**-0.48****	-0.33	-0.23	-0.12	**-0.43***	0.25	**0.41***	-0.01	0.10	**0.68*****		-0.19
RS_{cap}	0.02	-0.32	0.31	0.10	-0.02	0.13	-0.28	-0.17	0.01	-0.11	0.28	0.24	-0.11	0.20	0.26	0.01	

Notes: Abbreviations are as follows: specific leaf area, SLA; leaf dry matter content, LDMC; leaf area, LA; Leaf nitrogen content, N_{mass}; Leaf phosphorus content, P_{mass}; wood density, WD, dry season maximum diurnal leaf water potential, ψ_{max}; dry season diurnal variation in leaf water potential, ψ_{dv}; slope coefficient from the relationship between dry season predawn x midday leaf water potential, WR (water-regulation); Dry season stomatal conductance (g_{smax}); water-use efficiency based on leaf ^{13}C isotope composition, WUE; tree annual growth rate (GR); tree annual survival rate (SR); total number of resprouts, RS_{num}; length of longest resprout, RS_{len}; resprout relative growth rate, RS_{RGR}; species-specific resprout capacity, RS_{cap}.

FIGURES

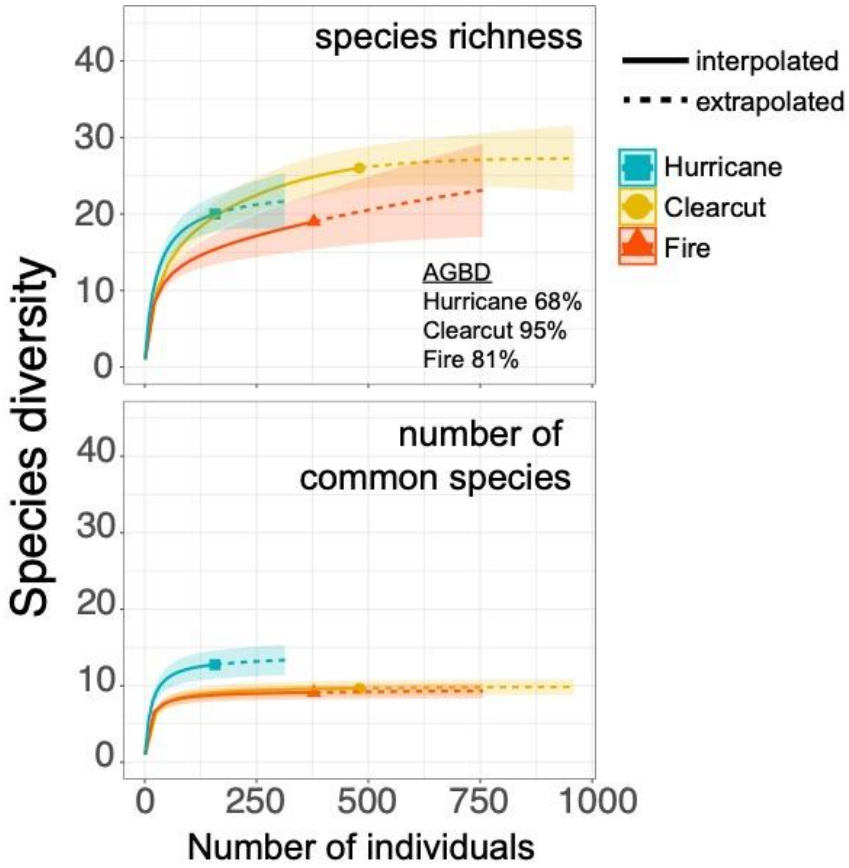

Figure 4.1. Sample-size-based rarefaction (solid line segment) and extrapolation (dotted line segment) of species diversity among resprouting individuals grouped by disturbance-type. Curves constructed by counting species equally without considering relative abundances (i.e. simply species richness) and by counting species in proportion to their abundances (i.e. number of common species in each assemblage) (bottom). Abbreviations include: average above-ground biomass destruction within each disturbance-type among the trees that resprouted and are included in this study, AGBD.

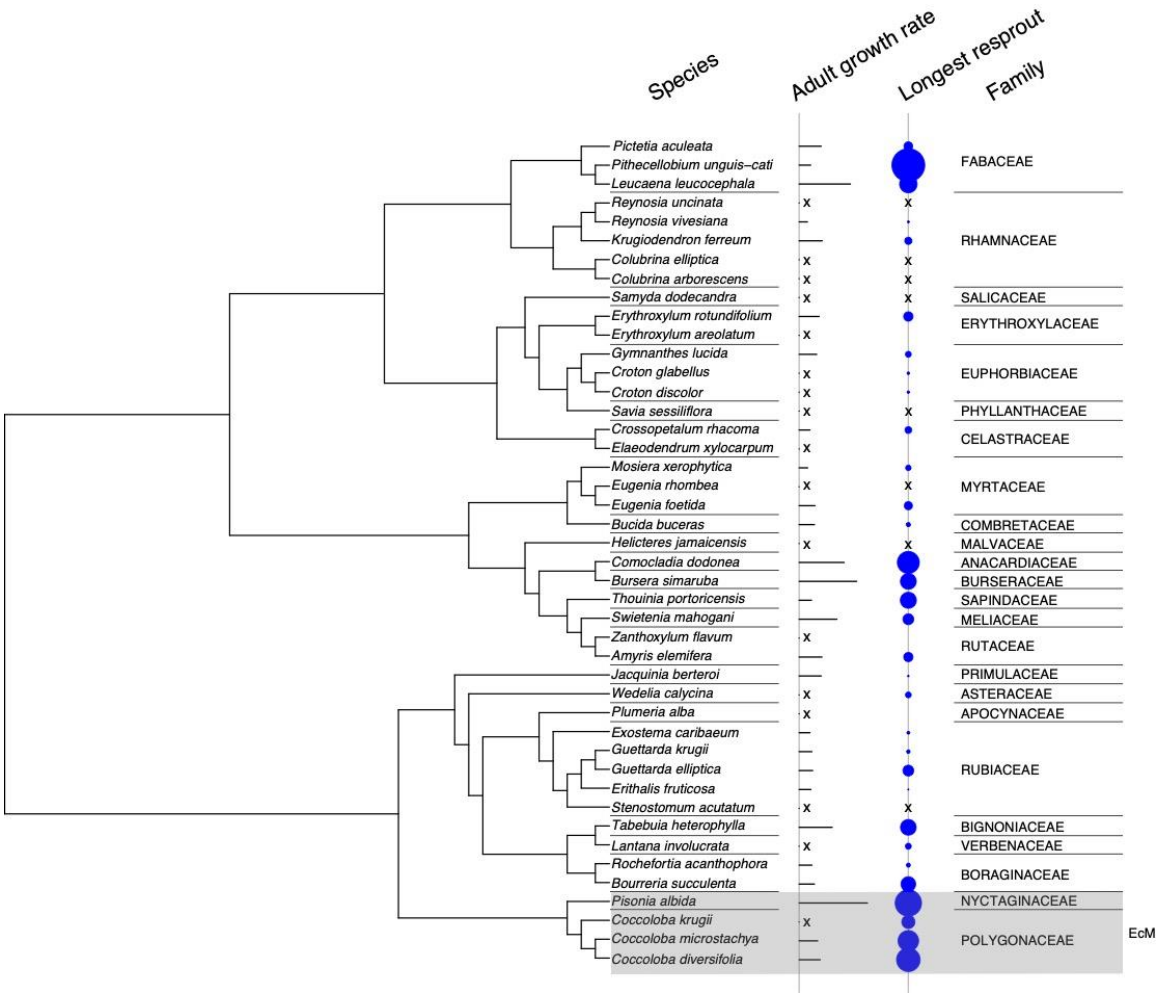

Figure 4.2. Phylogenetic tree of the 44 sampled tropical dry forest species in this study. Interspecific growth and median length of longest resprout are presented as standardized variables to aid comparability. Missing trait values are marked by an 'x'. Species known to possess ectomycorrhizal associations are shaded and marked by 'EcM'. Nomenclature follows Little & Wadsworth (1964) and *Gann et al.* (2015-2019).

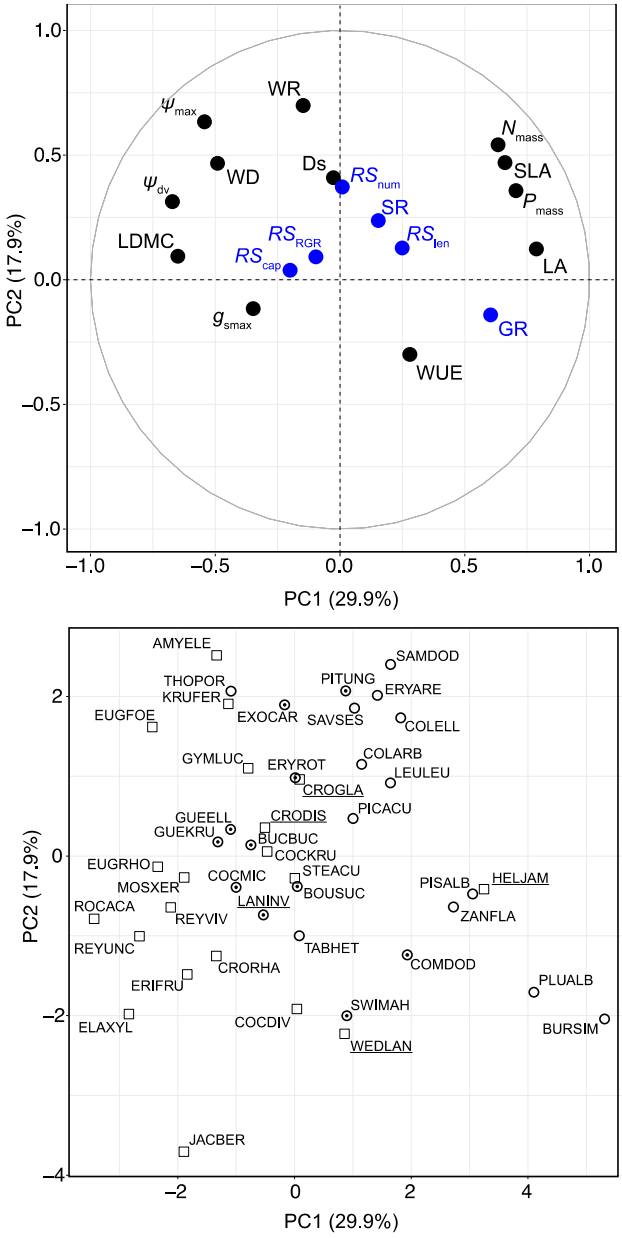

Figure 4.3. Biplots from our principal component analysis of 12 leaf and stem traits for 44 dry forest tree species. Variable loadings (top) show PC1 explained 29.9% of the total variation and PC2 explained 17.9% of the variation. Supplementary variables pertaining to growth, survival and resprouting were not included in the original analysis but correlated with axes post-analysis (represented by blue circles). Species loadings (bottom) are shown in respect to PC1 and PC2. Evergreen species are represented by open squares, true deciduous species by open circles and semi-deciduous species by dots encased with circles. Understorey woody shrubs are underlined.

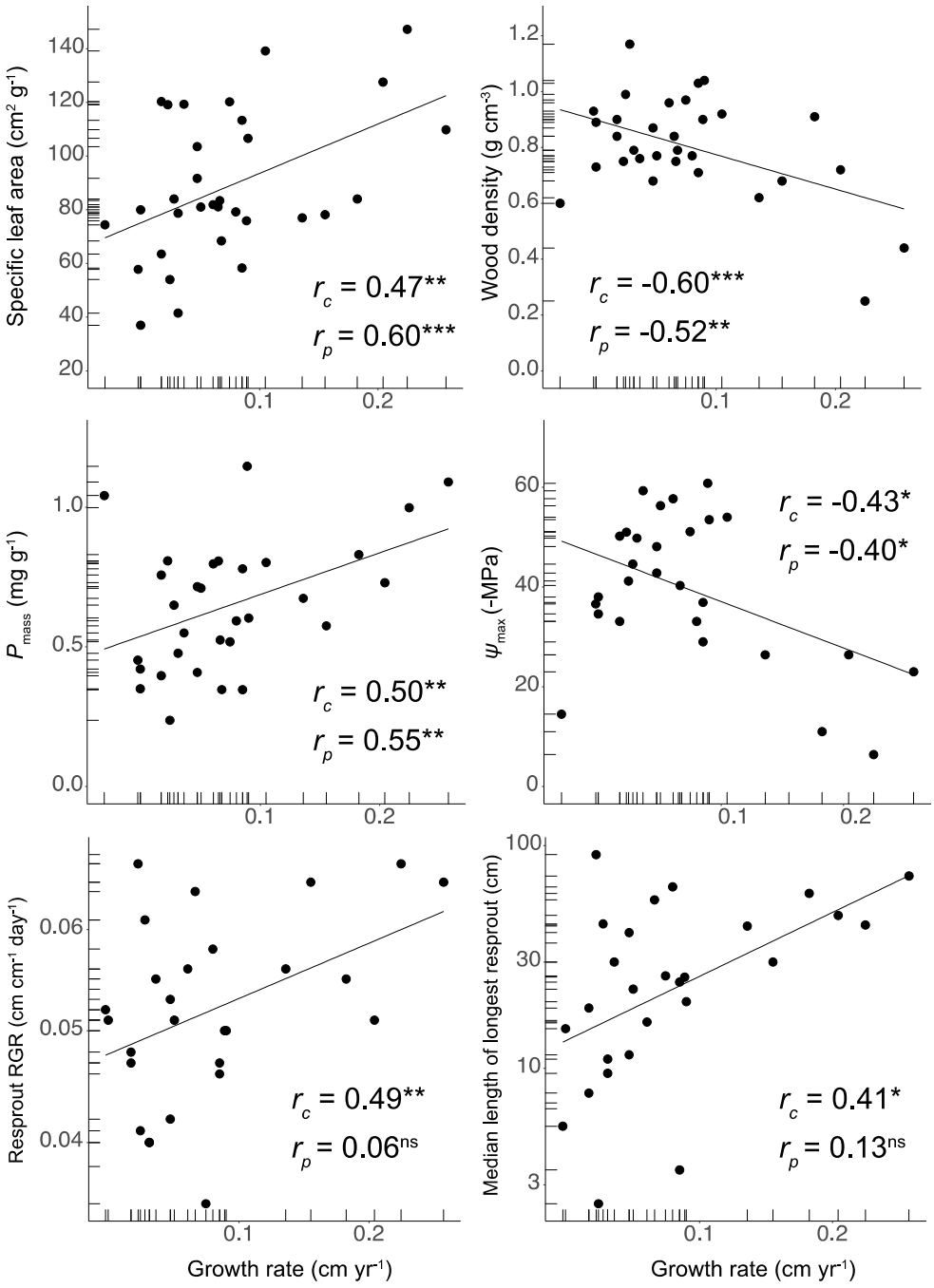

Figure 4.4. Leaf, stem and resprouting trait relationships with adult growth rate for dry forest tree species. Plots indicate the regression line, cross-species (r_c) and phylogenetically controlled (r_p) correlations and level of significance. *** p<0.001, ** p<0.01, * p<0.05, ns p>0.05. Axis rugs indicate variable distributions.

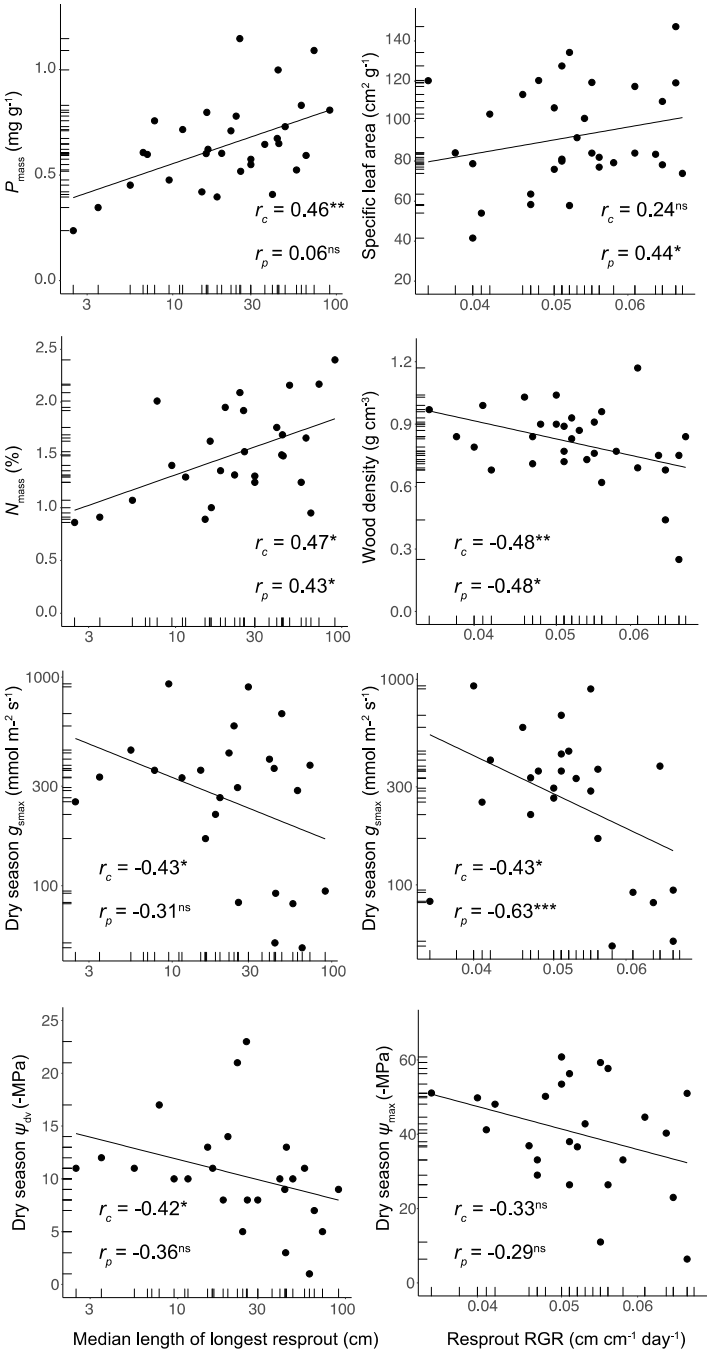

Figure 4.5. Leaf and stem trait relationships with resprouting properties for dry forest tree species. Plots indicate the regression line, cross-species (r_c) and phylogenetically controlled (r_p) correlations and level of significance. *** p<0.001, ** p<0.01, * p<0.05, ns p>0.05. Axis rugs indicate variable distributions.

CHAPTER FIVE

CLASSIFYING SHORT-TERM PHYSIOLOGICAL RESPONSES TO HURRICANE-INDUCED DEFOLIATION IN PUERTO RICAN DRY FOREST: SHORTCOMINGS TO USING LEAF HABIT.

ABSTRACT

1. In this study, we investigate whether a hurricane disturbance influenced trait plasticity in new leaves within a Puerto Rican tropical dry forest, including if responses differed by leaf habit-type.

2. We compared nine leaf traits important to dry forest resource economics and compared measurements from before and 1, 8 and 12 months after the hurricane. We chose 13 dominant tree species representing deciduous, semi-deciduous and evergreen leaf habits. Changes in interspecific vs intraspecific trait variance pre- vs post-hurricane were also determined.

3. One-month post-hurricane, large differences in leaf traits were found at the community level relative to pre-hurricane. New leaves were more resource acquisitive through higher stomatal conductance and specific leaf area but, in turn, displayed lower investment in physical and chemical structures. Similar directional shifts in traits were observed among leaf habit-types, but differences in the magnitude of trait change suggested hurricane events may affect leaf habit-types differently. Observed plastic responses were transient as pre-hurricane trait values returned after 8-12 months.

4. Plants exhibited significant trait plasticity in post-hurricane leaves suggesting an adaptation to recover from major physical disturbances. Ultimately however, high within-group variation meant leaf-habit was a poor classifier of species' responses within our tropical dry forest.

Key Words: tropical dry forest; functional traits; defoliation; wind; trade-offs; compensatory; physiology; leaf habit

INTRODUCTION

Predicting future carbon and water cycling in forests depends on understanding mechanisms of tree mortality and how functional and compositional dynamics in forests respond to large-scale physical disturbances that may intensify with climate change. Events that cause defoliation, for example herbivory or storm-related mechanical damage, have been shown to have impacts on forest growth, carbon gain, nutrient remobilization and source-sink relations (Singh & Singh, 1991; Iqbal *et al.*, 2012). Although defoliation initially impacts on plant fitness negatively, some plants are considered capable of exhibiting trait plasticity in remaining or new foliage presumably to counteract any negative effects (McNaughton, 1983; Collin, 2000; Schäfer, 2014). These physiological and morphological trait changes have become known as 'compensatory responses'. This characterization originates from the enhanced rate of carbon assimilation plants exhibit in order to compensate for leaf loss and therefore presumably enhanced growth rates or survival relative to defoliated plants that show no such response (McNaughton, 1983; Collin *et al.*, 2000).

To date, compensatory responses following defoliation have been well documented in both temperate (Lopushinsky & Klock, 1979; Oyama & Mendoza, 1990; Reich *et al.*, 1993; Vanderklein & Reich 1999; Schäfer, 2011) and tropical areas (Howe, 1990; Blundell & Peart, 2001; Ballina-Gomez *et al.*, 2010; Quentin *et al.*, 2011) and yet, our overall understanding of plant responses to defoliation remains weak (Schäfer, 2014). Much focus to date has been placed on greenhouse or field-based experimental designs involving the seedlings of a small number of species (usually only 1-2), however recent

evidence suggests that ontogenetic changes in function can be important, as younger plants may be more responsive to defoliation than adult trees (Boege, 2005). Additionally, to accurately determine responses at the ecosystem level requires canopy scale observations to be combined with leaf-level measurements (Schäfer, 2014). For example, overall reductions in carbon uptake at the canopy level linked to leaf area loss may in fact be mitigated by leaf-level compensations (Vanderklein & Reich, 1999; Schäfer, 2011). Finally, disturbance-related responses must be placed in context of broad changes in abiotic conditions (Ballina-Gomez *et al.*, 2010) for example, the large increases in water availability that accompany hurricane-induced defoliation. Many systems are also highly reliant on seasonal cycles of resource availability and therefore the timing of defoliation in relation to these resource-rich windows is also likely important to determining plant responses.

One of the primary goals behind improving our understanding of compensatory responses via trait plasticity is their incorporation into dynamic global vegetation models (DGVMs). Empirical data on compensatory responses is needed to better constrain the physiological parameters of current DGVMs (Raupach *et al.*, 2005; Schäfer *et al.*, 2014). At present these models generally fail to account for physical disturbances and the physiological responses they bring about in forest ecosystems (Bond *et al.*, 2005). A major challenge of models is how best to incorporate species-specific disturbance responses, in particular in highly biodiverse regions such as in the tropics. Parameterizing models according to individual species in biodiverse ecosystems is not practical, both logistically (too many traits to measure) and computationally. Therefore, finding a

reliable method to aggregate species in order to reduce the number of estimated parameters is necessary (Purves & Pacala, 2008).

Both continuous and discrete classifications have been proposed as methods to circumvent species-specific parameterization and simplify DGVMs. Continuous classifications utilize the well-established relationships between quantitative functional traits that represent the species life-history trade-offs structuring forest communities (Gilbert *et al.*, 2006). Such strategic axes including the leaf economic spectrum (Wright *et al.*, 2004) and the more recent, less developed wood economic spectrum (Chave *et al.*, 2009) are likely to form part of future models. Many current models however, adopt the approach of classifying species into discrete groups such as leaf habit (e.g. tropical broadleaf evergreen, tropical broadleaf deciduous) (Ostle *et al.*, 2009). This distinction is based upon the theory that different leaf habits are characterized by different sets of traits (Eamus, 1999; Reich *et al.*, 2007) and as such defined by different responses to environmental variation. For example, evergreens have a lower rate of return per (C) investment, as well as a higher cost of initial production and therefore they may be at a disadvantage when subjected to defoliation relative to deciduous species (Vanderklein & Reich, 1999). At the same time, longer leaf lifespans and less frequent leaf renewal may offset higher investment costs (Eamus, 1999; Kikuzawa & Lechowicz, 2011). Ultimately, significant gaps remain in our knowledge as previous attempts to determine responses among leaf habits have been constrained by low species numbers (usually one evergreen vs. one deciduous) as well as the often close phylogenetic relatedness among study species (Powers & Tiffin, 2010).

As a first step to categorizing species into functional groups for use in modelling ecosystem responses, interspecific trait variation must be greater than intraspecific trait variation within the community of interest (McGill *et al.*, 2006). Despite a body of evidence supporting interspecific diversity being significantly greater than at the intraspecific level (e.g. Markesteijn *et al.*, 2007; Hulshof & Swenson, 2010), recent large-scale trait studies encompassing all community individuals or a high number of populations along environmental gradients have challenged this view (Messier *et al.*, 2010; Albert *et al.*, 2010). Further complication stems from the view that higher intraspecific variation may be an important adaptation in response to environmental change (Malyshev *et al.*, 2016) and thus documenting ecosystem responses without incorporating within-species effects may result in the loss of important biological information. Furthermore, differing compensatory responses among traits and species may alter trait relationships as the factors shaping trait coordination change thereby complicating our ability to utilize functional trade-offs to capture the effects of biodiversity on forest function (Purves & Pacala, 2008; Cianciaruso *et al.*, 2009). Therefore, understanding the relative balance between interspecific vs. intraspecific variation will likely be informative in understanding ecosystem responses to climate change.

We took advantage of the close passing of Hurricane Maria to a tropical dry forest (TDF) in SW Puerto Rico to assess compensatory responses among 13 dominant tree species and determine the utility of leaf habit to categorize functional responses of species. TDFs offer a useful case study to observe how a nutrient and water efficient tree

community subjected to seasonal availability of resources responds to unexpected defoliation. On one hand, inherent trait plasticity in TDFs (Hulshof & Swenson, 2010) within and among species may enable individuals to maximize fitness in response to environmental variation. Plasticity may afford individuals to respond to reductions in canopy leaf area by enhancing resource acquisition in remaining or new leaves, particularly when resource availability is higher during the growing season. As such, we would expect trees to exhibit traits that confer higher than normal resource acquisition (i.e. compensatory responses) (Reich *et al.*, 1992). Alternatively, TDF systems may lack an enhanced response mechanism at the leaf level as a result of other unique evolutionary traits, namely the high incidence of cloning and high degree of nutrient recycling. For instance, the dominance of sprouting may introduce lower levels of genetic variation within populations thus reducing resistance to environmental stressors (Clarke *et al.*, 2013). Furthermore, for TDFs that are characterized by high rates of nutrient reabsorption and high root:shoot ratios (Lugo & Murphy, 1986), episodic defoliation may prevent the usual drawdown of nutrients that occurs prior to senescence and is used in leaf construction. As a result, post-hurricane leaves may be of lower quality relative to pre-hurricane leaves resulting in reduced resource acquisition rates.

Our overall goals were to evaluate short-term leaf-level physiological responses of dominant TDF species to defoliation from high winds, and the utility of leaf habit as a useful plant functional type to classify such responses. We tested the following hypotheses: (1) At the community level (all species combined), trait values of newly formed mature leaves will shift towards a strategy of resource acquisition; (2)

Interspecific trait variance is greater than intraspecific trait variance, and this is maintained immediately after the hurricane; (3) Leaf habit groups differ in their immediate trait response and the duration of their response following the hurricane. The relative shift towards resource acquisition would be less among evergreen species relative to deciduous species.

MATERIALS AND METHODS

SITE DESCRIPTION

Our study was conducted at the seasonally dry Guánica Commonwealth Forest, in southwest Puerto Rico (latitude 17°58'N; longitude 65°30'W). Mean annual air temperature is 25°C and mean annual precipitation is approximately 860mm (Murphy & Lugo, 1986b). Annual rainfall distribution is bimodal with the late rainy season (Aug-Nov) being the wettest period while an unreliable early rainy season often occurs during the spring (Apr-May). Inter-annual rainfall variability is high. In general, the landscape is dominated by exposed, jagged, limestone rock (karst) which forms part of the Poncé Limestone formation (Monroe, 1980), and is the dominant geology on this part of the island. Between limestone outcrops exist shallow mollisols with high organic matter content (23-30%; Murphy & Lugo, 1986b). The majority of the approximately 4400ha forest is composed of semi-deciduous vegetation with a gradual transition into scrub forest at lower elevations closer to the coastline. The forest has a complex land history which today has resulted in a mosaic of stands that vary in structure and composition (Molina Colon & Lugo, 2006). Puerto Rican TDF is composed of a higher proportion of

evergreen species (~50%) relative to other well-studied mainland TDFs (e.g. Guanacaste, Costa Rica and Yucatan, Mexico) as well as a relatively low proportion of Fabaceae species.

HURRICANE MARIA

Hurricane Maria, a Category 4 hurricane made landfall at the southeastern corner of Puerto Rico on 20th September 2017, travelling in a NW path across the island and re-entering the Atlantic Ocean near the town of Arecibo. Although wind speed was not captured by the upland USDA NRCS weather station located in the heart of the forest, a private weather station downwind captured a mean wind speed of 56.3 km/h and maximum wind gusts of 114km/h (WRCC, 2017). Considering the higher elevation and closer proximity to the direct path of the hurricane, our study sites likely experienced higher sustained winds as well as maximum wind gusts closer to the recognized Category 1 hurricane threshold (119 km/h). A substantial amount of rain fell over the hurricane period, with our study site receiving approximately 230mm of rain between 19-23rd September (Fig. 5.1; National Water and Climate Center, 2020).

CANOPY OPENNESS

As Guánica forest was affected by the outer bands of Hurricane Maria, we assessed differences in canopy openness from hemispherical photographs to confirm that canopy defoliation was both significant and widespread. Images were acquired from the NEON data portal for three forest plots located 0.5 – 1km from our study site. In total, 12 paired

images (pre- and post-Maria) were used from each of the three plots, taken at 4m intervals along both north-south and east-west transects. Percentage canopy openness was determined using Gap Light Analyzer V2.0 with the blue light filter and the 60_o ring (Frazer *et al.*, 1999). Our results confirmed that canopy openness effectively doubled from 14-20% pre-hurricane to 21.33-44.37% immediately after Maria (see Table 5.1 & Fig. 5.2). Differences among plots likely reflect the influence of topography and dynamic windfields.

SPECIES SELECTION AND MEASUREMENT OF PLANT FUNCTIONAL TRAITS

Thirteen dominant tree species (from nine families) were chosen, which together make-up 71% of the basal area in long-term data plots (Murphy & Lugo, 1986b). Species represent a range of leaf habits including 6 deciduous, 4 evergreen and 3 semi-deciduous species (Table 5.2). Defoliated individuals were chosen from the same area of the forest so as to minimize variation in physical damage from the hurricane.

We measured traits on the first fully-developed mature leaves produced after Maria (1 month post-hurricane; wet season), followed by new mature leaves collected ~8 months (dry season) and ~12 months (wet season) after the storm (Fig. 5.1). We only possessed pre-hurricane trait data from the winter dry season (February 2017) which we compared to post-Maria measurements. Our aim was for consistency among sample periods in the leaves we used for trait measurements, thus we ensured leaves originated from the same area of the canopy and were similar in their degree of maturity based on field experience and leaf position (typically the second leaf down from the apex).

Furthermore, we took care to avoid leaves showing signs of herbivory and age-related damage.

Nine leaf traits were chosen based on their importance to resource acquisition (e.g. carbon capture and water-use management), nutrient cycling and leaf structure (Table 5.3). Maximum stomatal conductance (g_{smax}) was measured using a steady-state porometer (SC-1, Decagon Devices, WA, USA) on five separate tagged leaves, for five trees per species (four for *Coccoloba diversifolia*). Multiple measurements were made between 06:00-14:00 as g_{smax} does not necessarily occur at midday for all species and also varies between seasons (Allerton & Van Bloem, *unpublished*; Medina & Cuevas, 1990). At the end of the day, chlorophyll content was determined for each of the 5 leaves used for g_{smax} by taking the average of three measurements per leaf from a chlorophyll content meter (Apogee, CCM-200). Leaves were then pooled into bulk samples (for each tree) and dried for 72hr at 75^{o}C prior to grinding. Ground leaves (n = 5 per species) were then sent to the Duke DEVIL laboratory and analysed for ^{13}C isotope and leaf nitrogen using a Carlo Erba NA1500 Elemental Analyzer (accuracy ±0.01%).

Morphological traits were measured on the same individual trees as for physiological traits. Between 5-10 leaves per individual were collected from terminal branches and that evening rehydrated overnight using distilled water and dark conditions. The following day, fresh mass was measured (precision balance ±0.001g) and leaves were scanned using a desktop scanner (Cannon MG3000, Tokyo, Japan). Leaf surface area (LA; cm^2) was calculated from scans and with the freeware ImageJ (Schneider *et al.*, 2012; https://imagej.nih.gov/ij/index.html). Samples were then oven-dried at 75^{o}C for

72hr before dry mass was determined. Specific leaf area (SLA; $cm^2\ g^{-1}$) was calculated as leaf surface area/ dry mass. Leaf dry matter content (LDMC; $g\ g^{-1}$) was calculated as dry mass／fresh mass. Stomatal density (Ds) was determined from 3 leaves for 5 individuals per species by creating microscope slides using nail varnish impressions of the abaxial (lower) leaf surfaces (Gitz & Baker, 2009). Stomata were then counted on slides using a LEXT OLS4000 laser microscope (5X-100X; Olympus, Japan). Earlier work determined all species concentrated stomata on the abaxial (lower) surface. The software ImageJ was used to count the number of stomata per mm^2. For most species, stomata were counted from 417315μm^2 surface area (range 67340-1643520μm^2)

STATISTICAL ANALYSIS

To test whether trees exhibited trait plasticity in response to partial defoliation, we fitted linear mixed models with each of our measured traits used as the outcome variable and with the fixed effects of sample date, leaf habit and their two-way interaction. For the purpose of modelling, a natural logarithm transformation was applied to five of our outcome variables including g_{smax}, CHL, SLA, LA, and Ds. Both LDMC and LNC were arscine transformed after conversion to proportional data. We tested the significance of fixed effects using F-tests and Kenward-Rogers approximations. This method has been shown to be most robust in the case of smaller sample sizes and less anti-conservative than the likelihood ratio test or Wald test thereby minimizing chances of Type I errors (Luke, 2017). Individual tree nested within species and season (wet, dry) were included in the random effects structure. We predicted that species may behave differently

according to sample date therefore we included random slopes for sample date by species (Barr *et al.*, 2013). The significance of random effects was tested including comparisons with null models using log-likelihood ratio tests and based upon Akaike's Information Criterion (AIC) with the most parsimonious model selected. Model diagnostics were performed by visual inspection of residual plots, revealing no clear violations of homogeneity of variance, normality, or linearity. To identify trait differences between sampling dates at the overall community and the leaf habit level, post-hoc Tukey HSD multiple comparison tests were implemented and considered significant at $p \leq 0.05$. To assess partitioning of interspecific and intraspecific variance in our traits, we used nested ANOVA's with random effects for each functional trait pre-hurricane and post 1 month (hypothesis 2; Messier *et al.* 2010). Variance partitioning was performed on each model using the 'varcomp' function in R (Paradis & Schliep, 2018). All analyses were analyzed using 'stats' (R Core Team, 2019), 'lme4' (Bates *et al.*, 2015) and 'emmeans' (Lenth, 2019) packages in R (version 3.5.3, R Core Team, 2019).

RESULTS

IMMEDIATE IMPACT OF THE HURRICANE ON NEW LEAF TRAITS AT THE COMMUNITY LEVEL

When compared with leaves measured before the hurricane, leaves produced 1 month post-hurricane exhibited a directional shift in trait values towards increased resource acquisition at the community level (Table 5.4, Table 5.5 & 5.6 for model results). On average, leaf-level g_{smax} increased by 58% (Tukey, $p<0.001$) but interestingly no increase

in ^{13}C discrimination was captured (Tukey, p=0.93) (Table 5.4). We observed changes to leaf structure immediately post-hurricane, with trees on average allocating less biomass per unit of leaf area (58% higher SLA; Tukey, p<0.001) and less biomass to structures overall (23% decrease in LA; Tukey, p<0.001). Mean leaf chlorophyll content, key to photosynthetic function, was also found to decrease by 36% on average post-hurricane (Tukey, p<0.001). Traits that showed no evidence of a response 1 month post-hurricane at the community level included $\delta^{15}N$, leaf nitrogen and stomatal density (Table 5.4). When wet season trait values collected 1 month post-hurricane were compared to wet season measurements made during the same month in 2018 (12 months post-hurricane), g_{smax}, SLA, LDMC, LA and CHL were all different (Tukey, p<0.01) suggesting that the responses we observed 1 month post-hurricane are not due to seasonal fluctuations in trait values alone.

INTERSPECIFIC VS INTRASPECIFIC VARIATION IN TRAIT RESPONSES

Before Hurricane Maria, interspecific variation explained a far greater proportion of the total variance compared to intraspecific variation for all our traits, but these differences narrowed after the storm (Table 5.7). The narrowing of differences was principally driven by three traits; SLA, LDMC and $\delta^{15}N$. Additionally, traits that exhibited some of the least plasticity immediately following the hurricane were also those with the lowest amount of intraspecific variation before and after the hurricane including Ds, LA, $\delta^{15}N$ and LNC (Table 5.4 & 5.7).

HOW DO LEAF HABIT GROUPS DIFFER IN THEIR IMMEDIATE RESPONSES?

Although the direction of change in traits pre-hurricane and 1 month post-hurricane was not different among leaf habits, the magnitude of change varied. The increase in g_{smax} immediately following the hurricane among all leaf habits was more pronounced for deciduous (+78%) and semi-deciduous (+46%) than for evergreen species (+35%) (Fig. 5.3) and the degree of overlap in g_{smax} decreased (Fig. 5.3). Increases in SLA were greatest among evergreen species in leaves 1 month post-hurricane but so were the decreases in foliar chlorophyll content compared to other leaf habit types. All groups showed comparable reductions in LDMC (Fig. 5.3). The leaf stomatal density of deciduous and evergreen species was higher 1 month post-hurricane relative to pre-hurricane levels (Fig. 5.3).

HOW SOON DO LEAF TRAITS RETURN TO PRE-HURRICANE LEVELS?

Of the traits found to exhibit short-term plastic responses, only leaf chlorophyll showed evidence of a delayed return to pre-hurricane values, specifically among true deciduous and true evergreen species (Fig. 5.3). Generally, all leaf habits returned to pre-hurricane values in other plastic traits after 8 months although in some cases returns surpassed the pre-hurricane value (e.g. g_{smax} was significantly lower 8 months post-hurricane compared to before the hurricane).

DISCUSSION

Overall, we found partial support for hypothesis (1) as large increases in g_{smax} and SLA at the community level were observed 1 month post-hurricane, suggesting a more acquisitive, water intensive mode of resource acquisition among species immediately following the hurricane. As the species in our study together comprise 71% of the total basal area in mature dry forest (Murphy & Lugo, 1986b), such compensatory responses likely have broad relevance to the overall functioning of our TDF community. Specifically the increases in gas-exchange we observed to hurricane-induced defoliation are similar to defoliation-induced compensatory responses documented in observational and experimental studies both in temperate and tropical regions, in particular in evergreen coniferous (Lopushinsky & Klock, 1979, Reich *et al.*, 1993, Vanderklein & Reich, 1999), deciduous upland oaks (Schäfer *et al.*, 2011) and tropical dry *Eucalyptus* species (Quentin *et al.*, 2011; Quentin *et al.*, 2012; Nolan *et al.*, 2014). Further, the results we found among our partially defoliated trees support previous findings that trees can exhibit strong enhancements in carbon gain without suffering massive losses in leaf area. For instance, stronger responses have been observed among partially defoliated relative to heavily defoliated evergreen *Pinus* and deciduous *Latrix* individuals (Reich *et al.*, 1993; Vanderklein & Reich, 1999).

The combination of a substantial increase in water availability delivered by Hurricane Maria (Fig 5.1) with a large increase in stomatal conductance exhibited by our trees underlines tight hydraulically-mediated control of gas-exchange. Water availability poses a major constraint to leaf gas-exchange in the dry tropics (Choat *et al.*, 2006) and

the positive relationship between g_s and soil-to-leaf hydraulic conductance is well reported in a number of systems (Sperry, 2000; Brodribb & Holbrook, 2004). Under well-watered conditions, trees vary K_{leaf} positively with transpiration so that the differential between ψ_{stem} and ψ_{leaf} remains small (Simonin *et al.*, 2015). Thus, as vapour-pressure deficit (VPD) increases during the daytime, ψ_{leaf} depressions are minimized, reducing constraints on g_s and photosynthesis. Additionally, shifts in plant water-use efficiency may not occur as transpiration is intrinsically linked to shifts in g_s and VPD (Wullschleger *et al.*, 1998), which is in agreement with the unchanged WUE observed among our trees (but see Reich *et al.*, 1993). The lack of a control in our study prevents us from categorically linking resource shifts to observed trait changes however, our findings generally align with the view that compensatory responses among TDF species following partial defoliation are aided by the increased availability of the principal limiting resource: water.

New leaves among trees were also characterized by lower LDMC, leaf area and chlorophyll content suggesting a reduction in leaf quality compared to before the hurricane. The timing of disturbance and its effect on internal resource storage (e.g. carbohydrates) may impact on the production of new leaves so soon after the first leaf flush of the wet season. Leaf flushing is an expensive process, and seasonal carbohydrate studies in the tropics have observed wet-season minima in total non-structural carbohydrate concentrations following leaf production (Newell *et al.*, 2002; but see Würth *et al.*, 2005). Defense allocations (i.e. higher LDMC within leaves) add even greater investment costs (Coley *et al.*, 1985; Sterck *et al.*, 2006), and have been linked to

reduced plant growth (Kitajima, 1996) possibly helping to explain the observed reduction in LA. Lower chlorophyll content in leaves may be partly explained by differences in chloroplast development between leaves measured pre-hurricane and 1 month post-hurricane. Although the new leaves we measured immediately following the hurricane were fully expanded, thylakoid stacking typically lags behind leaf growth thereby reducing the absorption capacity of young fully expanded leaves while full chloroplast development takes place (Kirk & Goodchild, 1972).

It is unclear from our initial findings whether the compensatory responses we observed have adaptive significance in terms of a positive effect on plant fitness (e.g. growth) in our TDF community. The large increases in gas-exchange and SLA in new leaves suggest that trees were able to enhance resource acquisition for the remainder of the growing season post-hurricane while water remained abundant. However, any predicted enhancement of photosynthesis may be compromised by the decline in leaf chlorophyll content. Whether such a reduction in radiation absorption is detrimental to tree health is unclear. It is well reported, particularly amongst agricultural crops that chlorophyll-deficient plants are capable of similar rates of photosynthesis as their "green" counterparts (Li *et al.*, 2013; Slattery *et al.*, 2017; Gu *et al.*, 2017). In such instances, a more even distribution of light within the mesophyll is attained in leaves with reduced chlorophyll content, which lessens non-photochemical quenching and thus improves photochemical efficiency (Sakowska *et al.*, 2018). In other words, for the same amount of energy absorbed or over the same amount of leaf area, more CO_2 can be fixed. Chlorophyll-deficient leaves in the larger crowns that characterize our trees may possess

an additional benefit of enhancing light transmittance of the upper crown layers therefore creating a more uniform illumination of the canopy and subjecting a lower portion to light saturation (Gu *et al.*, 2017; Walker *et al.*, 2018). The well-established relationship between SLA and relative growth rate may lead us to predict increases in productivity due to more light intercepted per unit mass (Lambers & Poorter, 1992; Wright & Westoby, 2000). However, this relationship is usually accompanied by higher leaf nitrogen concentrations reflecting higher concentrations of Rubisco and other photosynthetic proteins (Wright *et al.*, 2004) which we failed to observe. The large decrease in LDMC suggests that much of the increase in SLA may be driven by changes in leaf density as opposed to thickness. Chemical composition is an important determinant of leaf density (Lambers & Oliveira, 2019). However, as no simultaneous increase in LNC was observed among our trees, we suggest that increases in SLA are linked to lower fractions of sclerenchymatic tissue rather than larger cell sizes (Poorter *et al.*, 2009). Further, trees in our system may already possess sufficient internal N in what is a non-limited system (Murphy & Lugo, 1986b). The large decline in the proportion of LDMC may have consequences for trees and their ability to manage hydraulic stress during the following dry season. The lower fiber content decreases leaf hydraulic resistance, which may prevent leaves from working at their optimum and cause greater drought stress. Ultimately, despite the acquisitive direction of change observed in g_{smax} and SLA, the subsequent effect on plant fitness remains unclear due to observed changes in leaf quality that may impact the efficiency of the photosynthetic machinery as well as drought tolerance.

Generally, interspecific variation was substantially higher than intraspecific variation and remained so immediately following the hurricane thereby supporting hypothesis (2). Our results are in agreement with the increasing consensus that within tropical systems interspecific variation is large (Bonal *et al.*, 2000; Townsend *et al.*, 2007) and intraspecific differences of many commonly sampled leaf and wood traits generally account for around a quarter of the community trait variation (Hulshof & Swenson, 2010; Messier *et al.*, 2010; De Bello *et al.*, 2011). The finding that interspecific differences remain significantly larger than intraspecific differences in our TDF after hurricane disturbance supports the use of leaf habit as a species aggregator. We argue that further investigation is needed as our relatively low within-species sample sizes (n = 5) and use of standardized protocols mean our results may be underestimating the degree of species overlap (Violle *et al.*, 2012). Of note was the narrowing of differences between interspecific and intraspecific variation for SLA and LDMC one-month post-hurricane (Table 5.7). If this pattern is connected to the convergence of species' mean values of these traits then our ability to predict the effects of environmental change on TDF plant communities may increase (Ghalambor *et al.*, 2007; Malyshev *et al.*, 2016). Alternatively, if plastic responses of SLA and LDMC are proportionately higher than other correlated traits (e.g. leaf nitrogen) then this may impede our ability to utilize well-established functional trade-offs to capture the effects of biodiversity on forest function. Interestingly, many of our traits with the lowest amount of intraspecific variation including Ds, LA and $\delta_{15}N$ were also those that exhibited the weakest responses to the hurricane, supporting the view that low within-species variation inhibits species from

responding quickly and causing them to lag behind shifting optimal trait values (Henn *et al.*, 2018).

Leaf habit groups were generally similar in terms of which traits were found to be plastic and the direction of change in those traits, contradicting hypothesis (3). However, leaf habits did differ in the relative magnitude of trait changes suggesting differences in the degree of relative plasticity among leaf habits. The smaller compensatory response in g_{smax} among evergreen species compared to deciduous and semi-deciduous species may indicate a relative disadvantage although in TDFs, evergreens are documented as maintaining a lower, more constant level of gas-exchange across seasons (Sobrado, 1991; Eamus, 1999). Evergreen species also exhibited stronger relative declines in leaf quality including lower LDMC and chlorophyll content. As evergreens generally maintain their foliage for longer periods, such reductions in quality may impact on tree health. For example, lower LDMC and chlorophyll concentration could simultaneously reduce dry season drought tolerance and energy absorption. Greater relative declines in leaf structure among evergreens may be connected to differences in carbohydrate allocation patterns among leaf habits. Comparisons of carbohydrate concentrations between woody evergreen and deciduous species with close phylogenies have shown lower total non-structural carbohydrates (TNC) and greater proportional allocation of reserves to foliage in evergreens (Mooney & Hays, 1973; Newell *et al.*, 2002; Wyka *et al.*, 2016). The loss of reserves during the resource-abundant wet season may ultimately have little immediate consequence to productivity however there is evidence that trees favor using newly

produced photosynthates to drive growth (Vanderklein & Reich, 1999; Gessier & Treydte, 2016).

Despite the differences we observed in the magnitude of responses between leaf habits, these results do not support aggregating species by their leaf habits in order to categorize post-hurricane responses. The large variation in many of our traits resulted in a high degree of overlap among habits confounding attempts to separate responses. Ultimately, a high degree of biological information in respect to species-specific responses is being lost using this method, in particular in respect to deciduous habits (Fig. 5.3). Deciduous species in TDF are known to possess a broad range of trait combinations which may act to confound attempts to aggregate at the leaf habit level. A stark example is the likely advantage of possessing photosynthetic bark post-defoliation as in the case of the deciduous species *B. simaruba*. Our data are consistent with a number of TDF studies that have found large trait differences among species but high overlap among leaf habits (Prior *et al.*, 2003; Powers & Tiffin, 2010; Markesteijn *et al.*, 2011b).

Our study could be improved by increasing the spatial extent of sampled individuals across a greater extent of the dry forest zone. Trees sampled within a confined area likely share a higher degree of genetic similarity, in particular in our ecosystem where vegetative reproduction is the primary form of regeneration. Species that are predominantly clonal often have low levels of genetic variation within populations and therefore predicting their response to changing conditions requires an understanding of whether genetic variation confers resistance to environmental stressors. It is also critical to follow up these observations with demographic assessments of the community to

determine whether the compensatory responses we observed have adaptive significance. Sampling of root-growth and stem cores with time since hurricane may also help to determine whether reallocation of C reserves is taking place away from root and stem growth/ maintenance towards canopy recovery, and the relative implications that has among leaf habit groups.

CONCLUSION

In conclusion, our study is one of the few to have observed enhanced compensatory responses in response to partial defoliation among a large cohort of TDF species following a major hurricane event. We found significant enhancements in gas-exchange and SLA at the community level in mature new leaves produced after the hurricane however, leaves were also significantly poorer in quality which likely has implications for short-term drought resilience. Our use of leaf habit as a method to aggregate species responses was found to have significant limitations due to large within-group variation among species resulting in large overlaps between groups. That said, small differences between evergreen and deciduous groups lend support that evergreen species may be more adversely affected by defoliation due to the longer timescale plants will typically hold onto leaves with reduced quality. Post-hurricane trait responses have implications towards species compositional dynamics, carbon storage dynamics and plant-ecosystem resilience in the face of more intense/ frequent hurricane events from climate change.

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TABLES

Table 5.1. Percentage canopy openness two days prior and approximately one month after hurricane Maria in three NEON forest plots located close to our leaf sample sites in Guánica forest, Puerto Rico. Values are means of 12 hemispherical images collected at regular intervals across north-south and east-west transects. Paired t-tests were conducted on values before and after the hurricane within each plot.

Plot	Date	Sample points	Mean canopy openness (%)	SD	*t*	*p*
All	9/18/2017	36	17.43	6.43	-6.27	<0.001
	10/17/2017	36	34.81	14.63		
052	9/18/2017	12	14.27	3.49	-7.02	<0.001
	10/17/2017	12	38.73	10.82		
054	9/18/2017	12	19.96	8.71	-4.52	<0.001
	10/17/2017	12	44.37	13.71		
055	9/18/2017	12	18.06	5.00	-1.47	0.08
	10/17/2017	12	21.33	7.82		

Table 5.2. Species used in this study including their family, leaf habit and mean stem count. Semi-deciduous leaf habit refers to species that typically maintain most of their leaves well into the dry season until drought conditions become too intense. *Stem counts were collected from Allerton (*unpublished*) and Van Bloem et al. (2003) and lend insight into species growth form based on a continuum between shrub (more stems) and tree (less stems).

Family	Species	Leaf habit	Mean stem count*
Burseraceae	*Bursera simaruba*	Deciduous	1.0
Rubiaceae	*Exostema caribaeum*	Deciduous	1.2
Fabaceae	*Pictetia aculeata*	Deciduous	2.4
Nyctaginaceae	*Pisonia albida*	Deciduous	1.6
Bignoniaceae	*Tabebuia heterophylla*	Deciduous	6.5
Sapindaceae	*Thouinia portoricensis*	Deciduous	4.2
Boraginaceae	*Bourreria succulenta*	Semi-deciduous	1.5
Polygonaceae	*Coccoloba microstachya*	Semi-deciduous	6.1
Rubiaceae	*Guettarda krugii*	Semi-deciduous	3.4
Rutaceae	*Amyris elemifera*	Evergreen	1.5
Polygonaceae	*Coccoloba diversifolia*	Evergreen	3.1
Rubiaceae	*Erithalis fruticosa*	Evergreen	4.4
Euphorbiaceae	*Gymnanthes lucida*	Evergreen	1.5

Table 5.3. Physiological, biochemical and morphological traits measured in this study and their functional role.

Trait	Units	Abbreviation	Functional role
Maximum rate of stomatal conductance	mmol m^{-2} s^{-1}	g_{smax}	Carbon gain and water-use
^{13}C isotope composition	‰	$\delta^{13}C$	Water-use efficiency
Specific leaf area	cm^2 g^{-1}	SLA	Carbon gain, structural investment
Leaf area	cm^2	LA	Carbon gain, structural investment
Stomatal density	no. mm^2	Ds	Carbon gain and water-use
Leaf dry matter content	g g^{-1}	LDMC	Structural investment, physical resistance
Leaf nitrogen content	%	LNC	Carbon gain, structural investment
^{15}N isotope composition	‰	$\delta^{15}N$	N cycling, N-fixation
Leaf chlorophyll content	µmol m^{-2}	CHL	Photosynthesis

Table 5.4. Differences in the mean, minimum, maximum and coefficient of variation (CV) before and immediately following Hurricane Maria for nine community-level traits (all 13 species pooled). Measurements were made 7 months prior during a winter dry season (-7mo.) and 1 month after (+1mo.) the hurricane during the rainy season. Trait abbreviations the same as Table 5.3. *p-values refer to the Tukey pairwise contrast between pre-hurricane and post-1 month from our linear mixed model (Full results see Tables 5.5 & 5.6)

	Mean			Minimum		Maximum		CV (%)	
Trait	Pre Dry	Post 1mo. Rainy	Tukey HSD p-value*	Pre Dry	Post 1mo. Rainy	Pre Dry	Post 1mo. Rainy	Pre Dry	Post 1mo. Rainy
Physiological									
g_{smax} (mmol m^2 s^{-1})	320.2	504.8	**<0.001**	63.7	292.5	909.8	795.6	61.6	26.7
$\delta_{13}C$ (‰)	-28.7	-28.8	0.93	-30.8	-31.4	-26.4	-26.3	2.9	3.3
Biochemical									
LNC (%)	1.96	2.07	0.68	0.65	1.08	3.2	3.73	25.3	29.6
CHL (µmol m^{-2})	451.5	289.0	**<0.001**	264.6	135.3	734.4	618.6	23.5	38.6
$\delta_{15}N$ (‰)	2.37	2.67	0.67	-3.10	-4.00	6.20	6.60	82.6	64.9
Morphological									
SLA (cm^2 g^{-1})	93.4	147.3	**<0.001**	41.8	74.6	179.0	266.6	28.0	16.9
LDMC (g g^{-1})	0.42	0.28	**<0.001**	0.26	0.17	0.66	0.38	18.9	17.1
LA (cm^2)	23.6	18.2	**<0.001**	5.5	4.8	141.7	120.5	98.6	108.9
Ds (no. mm^2)	219.3	263.0	0.90	90.5	91.3	472.8	524.8	49.2	47.5

Table 5.5. Linear mixed model results assessing differences in trait values according to sample date, leaf habit and their interaction. Species was included as a random effect in our model. Values were determined via Kenward-Rogers approximation. *p*-values in bold are significant to $\alpha = 0.05$. Trait abbreviations follow those found in Table 5.3.

		Fixed effects		
Trait parameter		Date	Leaf habit	Date x Leaf habit
Physiological				
g_{smax}	F	60.42	0.92	2.555
	p-value	**≤0.001**	0.429	**≤0.05**
$\delta_{13}C$	F	21.78	1.03	3.99
	p-value	**≤0.001**	0.392	**≤0.001**
Biochemical				
LNC	F	29.55	3.83	2.60
	p-value	**<0.001**	0.058	**<0.05**
CHL	F	60.21	2.25	4.28
	p-value	**<0.001**	0.156	**<0.001**
$\delta_{15}N$	F	4.86	0.09	6.18
	p-value	**<0.01**	0.912	**<0.001**
Morphological				
SLA	F	126.66	3.37	6.34
	p-value	**<0.001**	0.076	**<0.001**
LDMC	F	158.35	0.70	0.521
	p-value	**<0.001**	3.373	**<0.01**
LA	F	14.58	0.91	1.93
	p-value	**<0.001**	0.434	0.076
Ds	F	10.09	1.456	2.410
	p-value	**<0.001**	0.283	**<0.05**

Table 5.6. Post-hoc comparisons of trait values between sample-dates from our linear mixed model analyses. The estimated size of difference between sample-dates (Est) was back-transformed for g_{smax}, CHL, SLA, LA, Ds (from log scale) and LNC (from arcsine scale) (Laursen et al. 2014). *p*-values in bold are significant to $\alpha = 0.05$. Trait abbreviations as in Table 5.3. *The back-transformation of log values estimates the ratio of the mean response (e.g. Pre-hurricane g_{smax} was estimated to be 1.82 times lower than g_{smax} one month post-hurricane). All other estimates are on the original scale.

	Physiological				Biochemical					
	g_{smax} (log)		$\delta_{13}C$		$\delta_{15}N$		LNC (arcsine)		CHL (log)	
Sample date contrast	Est*	*p*-value	Est	*p*-value	Est	*p*-value	Est	*p*-value	Est*	*p*-value
Pre – Post 1mo.	-1.82	**≤0.001**	0.09	0.93	-0.18	0.67	-0.06	0.68	1.63	**≤0.001**
Pre – Post 8mo.	2.10	**≤0.001**	-0.60	**≤0.001**	-0.57	**≤0.01**	0.34	**≤0.001**	1.19	**≤0.001**
Pre – Post 12mo.	1.05	0.95	-0.94	**≤0.001**	-0.43	**≤0.05**	0.21	**≤0.001**	1.20	**≤0.001**
Post 1mo. – Post 8mo.	3.82	**≤0.001**	-0.69	**≤0.001**	-0.38	0.08	0.40	**≤0.001**	-1.38	**≤0.001**
Post 1mo. – Post 12mo.	1.92	**≤0.001**	-1.03	**≤0.001**	-0.25	0.39	0.27	**≤0.001**	-1.36	**≤0.001**
Post 8mo. – Post 12mo.	-1.99	**≤0.001**	-0.34	0.10	0.13	0.83	-0.13	**≤0.05**	1.01	0.99

	Morphological							
	SLA (log)		LDMC		LA (log)		Ds (log)	
Sample date contrast	Est*	*p*-value	Est	*p*-value	Est*	*p*-value	Est*	*p*-value
Pre – Post 1mo.	-1.67	**≤.001**	0.16	**≤0.001**	1.27	**≤0.001**	-1.03	0.90
Pre – Post 8mo.	1.02	0.89	-0.02	0.08	1.31	**≤0.001**	-1.14	**≤0.05**
Pre – Post 12mo.	-1.08	**≤0.05**	0.05	**≤0.001**	1.06	0.59	1.09	0.28
Post 1mo. – Post 8mo.	1.70	**≤0.001**	-0.18	**≤0.001**	1.03	0.93	-1.11	0.06
Post 1mo. – Post 12mo.	1.54	**≤0.001**	-0.11	**≤0.001**	-1.20	**≤0.01**	1.13	**≤0.05**
Post 8mo. – Post 12mo.	-1.11	**≤0.01**	0.07	**≤0.001**	-1.23	**≤0.001**	1.25	**≤0.001**

Table 5.7. Percentage contribution of interspecific (Species) and intraspecific (Tree) variation of nine functional traits before and immediately following (post-1 month) Hurricane Maria among 13 Puerto Rican TDF species. Variance partitioning was conducted from a full nested linear model for each trait. When appropriate, data was transformed to their natural log (except LNC which were arscine transformed). *N* = 65 trees. Square brackets indicate 95% confidence intervals, calculated by bootstrapping (500 runs with 65 randomly sampled data points with replacement).

	Ecological scale and sample date			
	Species		Tree	
Trait	Pre	Post 1mo	Pre	Post 1mo
Physiological				
log g_{smax}	84 [80-93]	87 [84-96]	12 [9-22]	10 [9-22]
$\delta_{13}C$	66 [55-87]	61 [54-83]	28 [13-31]	32 [19-33]
Biochemical				
$\delta_{15}N$	84 [79-94]	70 [62-91]	12 [8-27]	24 [10-33]
arc LNC	82 [79-93]	86 [83-93]	14 [9-24]	11 [9-19]
log CHL	70 [64-86]	70 [64-85]	24 [15-32]	24 [17-30]
Morphological				
log SLA	77 [73-88]	42 [41-75]	18 [13-27]	49 [28-55]
LDMC	73 [69-88]	59 [53-83]	22 [14-30]	34 [19-33]
log LA	88 [73-89]	82 [49-84]	9 [8-22]	14 [13-32]
log Ds	91 [90-96]	92 [93-97]	6 [6-13]	5 [6-13]

FIGURES

Figure 5.1. Biweekly rainfall and soil moisture percentage over the course of the study period in Guánica forest, Puerto Rico. Hurricane Maria made landfall in south east Puerto Rico on September 20th 2017 as a Category 4 storm on the Saffir-Simpson scale and travelled in a north westerly direction across the island. Guánica forest was hit by the outer bands of the hurricane, bringing Category 1 winds and a deluge of rainfall. Arrows represent functional trait sampling dates of leaves : (1) "Pre-hurricane"; (2) "Post 1mo."; (3) Post 8mo.; (4) Post 12-mo. Rainfall and soil moisture data was obtained from USDA NRCS. www.wcc.nrcs.usda.gov/nwcc/site?sitenum=2067.

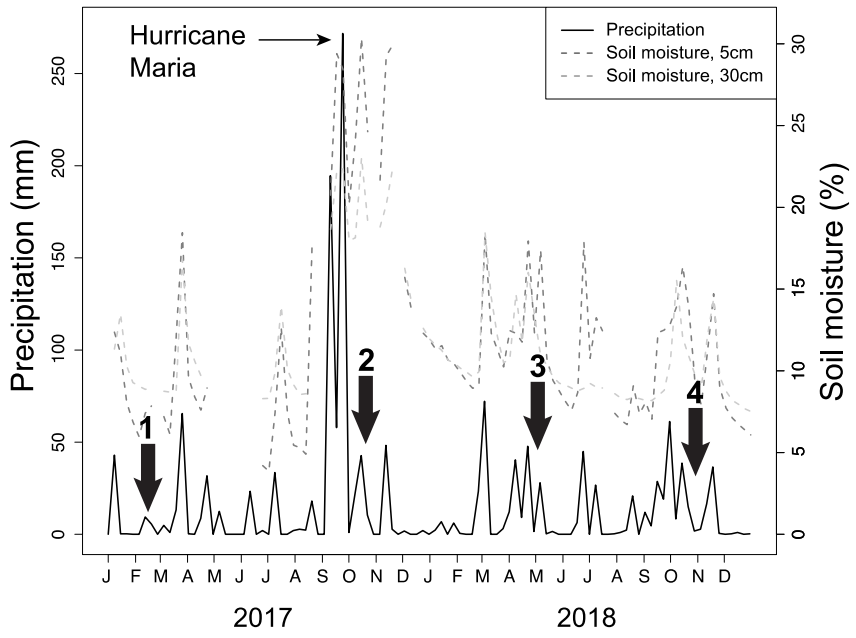


Figure 5.2. Percentage canopy openness before and after hurricane Maria in three NEON forest plots in Guánica forest, Puerto Rico. Value in parenthesis represents *p*-value for paired t-test before and after hurricane Maria.

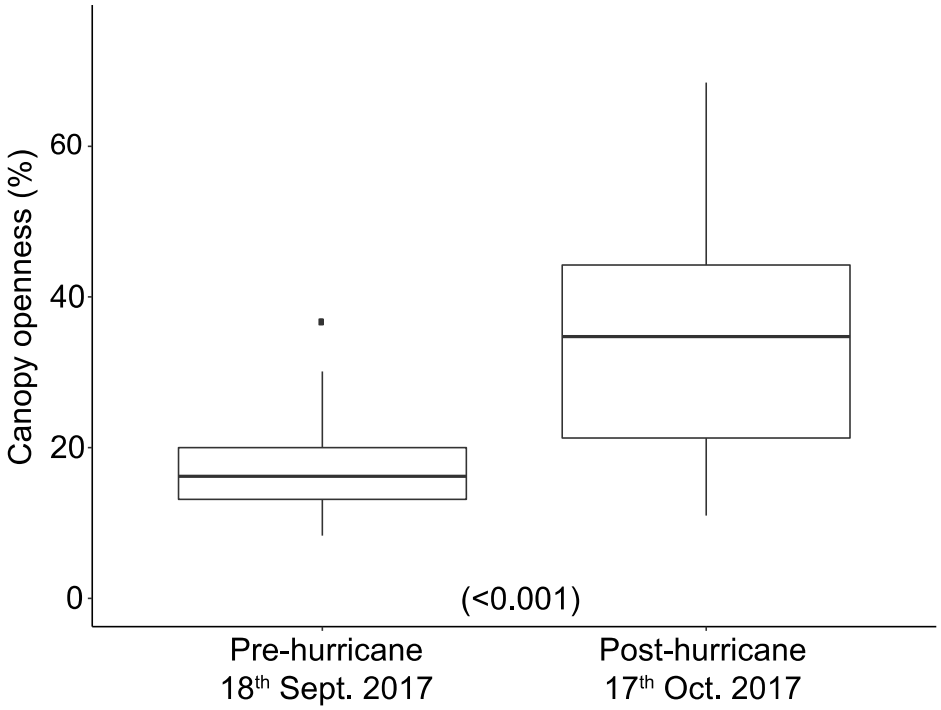
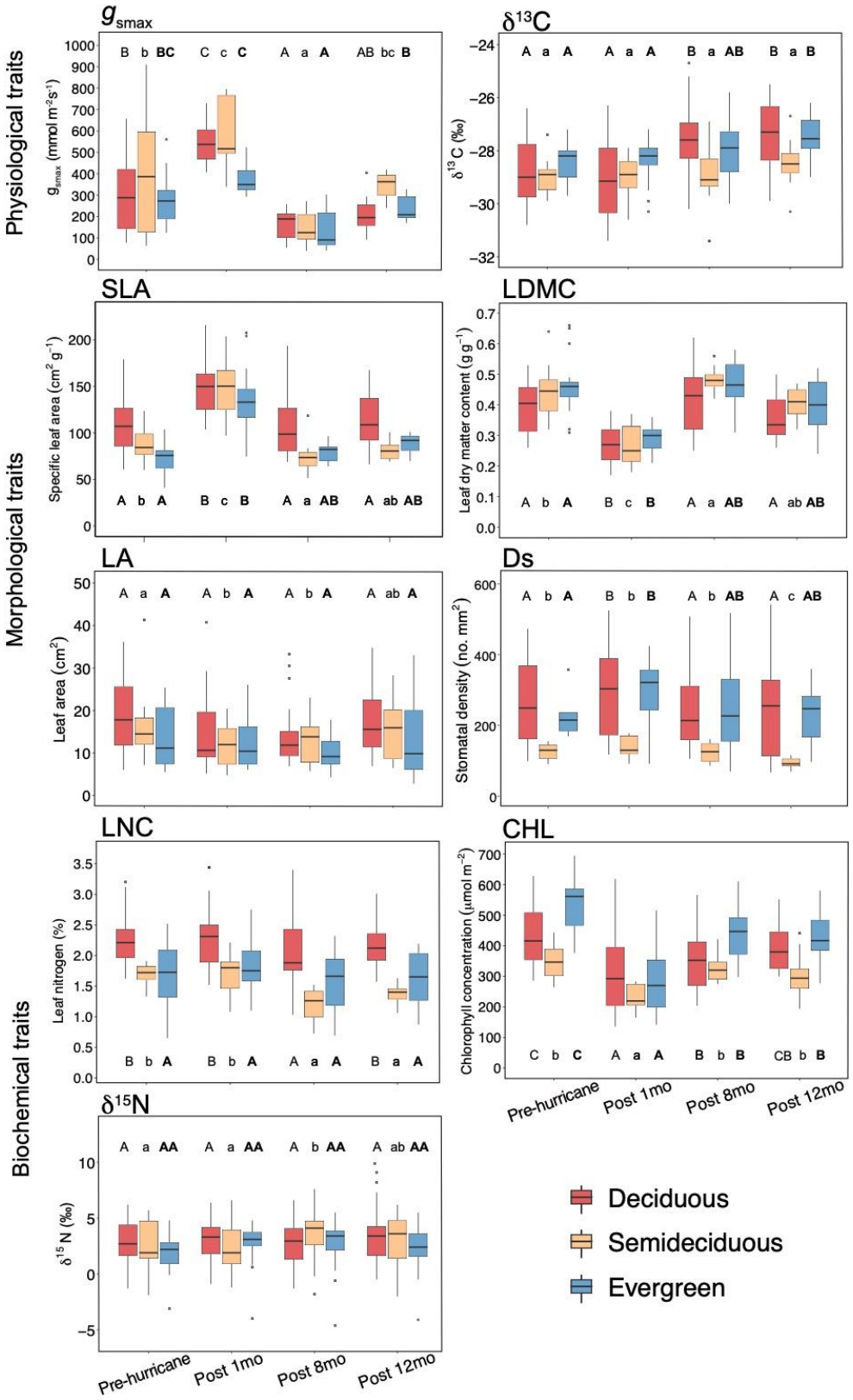


Figure 5.3. Distributions of physiological, morphological and biochemical traits by leaf habit group across our four sampling dates. Letters refer to Tukey HSD post-hoc comparison tests within each leaf habit group and between sampling dates from our linear mixed models (Full results in Supplementary materials). Post-hoc letter fonts relate to leaf habits as follows: (A) Deciduous; (a) Semi-deciduous; (**A**) Evergreen. Trait abbreviations are found in Table 5.3.


Physiological traits
Morphological traits
Biochemical traits
g_{smax}
g_{smax} (mmol m^{-2}s^{-1})
B b BC
C c C
A a A
AB bc B
δ^{13}C
δ^{13}C (‰)
A a A
A a A
B a AB
B a B
SLA
Specific leaf area (cm^2 g^{-1})
A b A
B c B
A a AB
A ab AB
LDMC
Leaf dry matter content (g g^{-1})
A b A
B c B
A a AB
A ab AB
LA
Leaf area (cm^2)
A a A
A b A
A b A
A ab A
Ds
Stomatal density (no. mm^2)
A b A
B b B
A b AB
A c AB
LNC
Leaf nitrogen (%)
B b A
B b A
A a A
B a A
CHL
Chlorophyll concentration (µmol m^{-2})
C b C
A a A
B b B
CB b B
δ^{15}N
δ^{15}N (‰)
A a AA
A a AA
A b AA
A ab AA
Pre-hurricane
Post 1mo
Post 8mo
Post 12mo
Deciduous
Semideciduous
Evergreen

CHAPTER SIX

CONTRASTING COMMUNITY ASSEMBLY MECHANISMS DRIVE TROPICAL DRY FOREST REGENERATION FOLLOWING CLEARCUTTING AND FIRE.

ABSTRACT

1. Understanding how environmental and biological factors drive forest succession continues to be a primary focus of community ecologists. Tropical forests are under increasing threat from various human-caused disturbances, that can range in their impacts and consequences for forest function. Yet our understanding of the mechanisms driving successional trajectories among disturbance-types remains limited, especially in cases where resprouting dominates post-disturbance regeneration.

2. We censused species across a 47-yr clearcut and 34-yr fire chronosequence and collected ten traits related to resource economics and resprouting in a Puerto Rican tropical dry forest community. The community-weighted trait distributions were quantified including the community-weighted mean, variance and trait range to determine the relative contribution of different assembly mechanisms to recovery post-disturbance. Trait distributions were weighted by both abundance and basal area to determine whether different weighting factors were important to different disturbance types.

3. Over time, community-weighted means showed both clearcut and fire communities exhibited shifts in functional strategy from resource conservation to resource acquisition, but fire sites showed a much greater rate of change. Positive shifts in leaf area, leaf nitrogen content and leaf phosphorus content across succession were observed in both disturbance-types but only clearcut sites displayed decreases in drought tolerance including lower WD and less negative maximum leaf water potential.

4. We found evidence that simultaneous multiple assembly processes were driving succession in both clearcut and fire sites. The abiotic filter appeared to promote high

functional similarity in drought tolerance (low ψ_{max}) in clearcut sites and resource conservation (low SLA and $\delta_{13}C$) in fire sites. But evidence of strong filtering was not observed and resprouting from remnant below-ground structures suggested the maintenance of pre-disturbance partitioning of below-ground resources. Disturbance-types showed contrasting assembly mechanisms in later succession. There was an increase in biotic interactions and concurrent decrease in the abiotic filter in later successional clearcut sites. Patterns in fire sites were consistent with an increase in abiotic constraints or development of competitive hierarchies which may be linked to the invasion of African pasture grasses. Evidence for facilitative interactions between quick growing 'nurse' species and other native trees was also found in older fire communities. 5. These findings are evidence that when disturbances are less severe such as small-scale clearcutting, resprouting results in the fast recovery of functional diversity by enabling much of the pre-disturbance community to persist. Tropical dry forests do not appear resilient to fire, as the strength of abiotic factors or competitive interactions over time inhibit regrowth and restrict tree establishment to fast-growing drought avoidant species that can compete with grasses. This study underlines the complexities of dry forest assembly and the dramatically different outcomes in recovery following different disturbance-types.

Keywords: resprouting, Puerto Rico, abiotic filtering, functional traits, chronosequence, disturbance, fast-slow, succession

INTRODUCTION

Tropical forests are the focus of anthropogenic land-use change (Hansen *et al.,* 2013) leading to much of their area existing in a state of secondary succession (Wright, 2005). Tropical dry forests (TDFs) are particularly vulnerable to degradation due to their fertile soils and distribution within favorable climates, with the result being loss of biodiversity and alterations to ecosystem processes and function (Murphy & Lugo, 1986a; Blackie *et al.*, 2014). The impact on ecosystem function and the rate and trajectory of recovery is strongly related to the type, severity, frequency and timing of disturbance (Foley *et al.*, 2005; Mouillot *et al.*, 2013). Tropical dry forests have shown remarkable resilience and somewhat predictable recovery trajectories following long-term land-use changes such as agriculture and pasture use where forest succession essentially begins from zero and recolonization via seed dispersal is the principal form of regeneration (Lohbeck *et al.*, 2013; Becknell & Powers, 2014; Buzzard *et al.*, 2016). Other short-term 'rapid' disturbances such as fire and clearcutting however, tend to occur without resetting succession back to stand initiation and are spatially and temporally diffuse in their impacts - often killing individuals or patches of trees, inducing mortality over years rather than immediately and preserving bud banks for resprouting (Cochrane *et al.*, 2009; Pyles *et al.*, 2018; Cohen *et al.*, 2016; Clarke *et al.,* 2013). As such, these events may have functionally distinct consequences during succession that differ in their predictability based on established successional theory.

Although taxonomic approaches can be useful in describing disturbance effects (e.g. Connell, 1978), functional approaches may perform better in predicting successional

trajectories and mechanisms driving vegetation change (Díaz *et al.*, 2004; Vandewalle *et al.*, 2010). Here, a trait-based approach scaled up to the community level can offer insight (McGill *et al.*, 2006). During succession, species replacement is often explained by an increase in site productivity as plant physiological strategies respond to local shifts in resource dynamics and reductions in environmental stressors (Diaz *et al.*, 2004; Wright *et al.*, 2005; Grime, 2006). Species' strategies can be determined based upon their positioning along a continuum of functioning related to an axis of resource acquisition and conservation (Garnier *et al.*, 2015). So called 'slow' strategies are characterized by slower rates of tissue turnover and traits that promote water and nutrient conservation and 'fast' strategies are associated with faster tissue turnover, high resource capture potential and fast growth (i.e. a fast-slow trade-off) (Díaz *et al.*, 2004; Reich, 2014). To a large extent, soil water availability drives ecosystem productivity in TDF and varies considerably between successional stages (Lebrija-Trejos *et al.*, 2011; Pineda-Garcia *et al.*, 2013). For instance, exposed early successional sites tend to be hot and dry whereas closed canopy late successional sites are cooler and relatively humid. Assuming a positive shift in resource availability with succession, a concurrent directional shift in the mean community phenotype may be observed as 'slow' plant strategies (e.g. small, thick leaves with low specific leaf areas and high wood density) associated with stressful, unproductive early successional sites shift to 'fast' strategies (e.g. large, inexpensive leaves with high specific leaf area and N content and low wood density) in later successional sites (Grime, 2006), although this appears to contradict typical successional theory in the tropics (Chazdon, 2013).

Conceptually, the mechanisms driving succession are determined by a set of hierarchical filters (i.e. abiotic, biotic, stochastic), that select species from the regional pool based upon their traits (Fig. 6.1, top) (Keddy, 1992; Hubbell, 2001). The physical constraints that exist in stressful, unproductive early successional sites should increase the influence of the abiotic filter and lead to a reduced trait range (Fig. 6.1, middle) and high functional similarity (i.e. a convergence in the trait distribution; Fig. 6.1, bottom left) as only a limited number of species are able to persist (Weiher *et al.*, 1998; Cornwell *et al.*, 2006). Such patterns may not always be clear however due to the heterogenizing effect of stochastic dispersal processes (Hubbell, 2001). Furthermore, detecting an abiotic filter may be challenging in TDFs where certain guilds are known to possess a wide range of trait combinations to maximize fitness under harsh conditions (e.g. water-use traits among early site colonizers). In later successional communities by contrast, a divergence in trait values should be apparent as site productivity increases and environmental constraints weaken (Fig. 6.1, bottom right). Such trait patterns could be interpreted as a sign of species coexistence through niche partitioning as competitive trade-offs develop (MacArthur & Levins, 1967; Weiher *et al.*, 1998; Grime, 2006). However, divergent trait patterns among coexisting species may also be an indication of facilitation within stressful environments as "nurse plants" aid the establishment of other species by modifying the nearby microclimate (Callaway *et al.*, 2000). Here, a two-step approach incorporating multiple metrics that include the trait range and variability distributions may help elucidate mechanisms driving succession within disturbed communities (Bernard-Verdier *et al.*, 2011).

Regeneration traits are part of a suite of components (including disturbance and environmental characteristics) responsible for informing community assembly outcomes (Lavorel & Garnier, 2002). In this regard, resprouting is an important but neglected niche often omitted from trait-based studies (Clarke *et al.* 2013). Interspecific resprouting capacities have a critical influence on demographic processes (e.g. survival, recruitment, growth) thereby helping to shape the relative contribution of species post-disturbance. Species turnover is generally less after disturbance in resprouting habitats relative to where seed dispersal is dominant, so changes in species composition along the successional gradient may be harder to detect (Quesada *et al.,* 2009). Therefore, disturbance-based studies in high resprouting habitats pose interesting methodological questions on how to quantify species' relative contribution in order to detect assembly processes. For instance, using basal area or abundance will shift the contribution to plot biomass from fast growing resprouts on surviving stumps relative to slower growing seedlings. Therefore, determining species relative contributions to community level functional strategies using both a basal area- and abundance-weighted approach will provide insight into optimal ways to assess functional development during succession in high resprouting environments.

Here, using a 'space-for-time' approach we constructed two distinct chronosequences up to 47 years long based on previously clearcut or burnt sites in order to assess functional recovery in Puerto Rican TDF. In total, 10 functional traits were selected linked to resource capture and regeneration and informative vis-à-vis the 'fast-slow' trait continuum. A total of 41 tree species were assessed in 21 sites. We asked three

questions: (i) How does functional recovery proceed in communities subjected to clearcutting and fire, (ii) What mechanisms of assembly drive TDF succession in clearcut and fire sites where resprouting is dominant?, (iii) How do trait weighting-factors affect detection of assembly patterns in the two disturbance chronosequences (i.e. abundance vs. basal area)? We hypothesized that: (i) Clearcut sites would exhibit the transition from 'slow' traits in early successional communities to 'fast' traits in late-successional communities. Fire sites will show predominantly 'slow' conservative traits along the whole successional gradient as harsh physical conditions perpetuate due to fire legacy effects; (ii) In clearcut communities, abiotic filtering (i.e. trait convergence) will dominate in early-successional sites, while biotic filters (i.e. trait divergence) become influential in later-successional communities. In fire communities however, abiotic filtering (i.e. reduced ranges and trait convergence) will dominate across the chronosequence; (iii) Mean functional strategies in clearcut sites will be driven by a diverse set of demographic forces including fast growth of survivors through resprouting, mortality and recruitment and therefore both abundance and basal weightings will demonstrate trends in the community-weighted mean and variance. Fire will act as an equalizing force in our maladapted TDF and therefore post-fire succession will be slow and restricted to a subset of sprouters and seeders. Therefore, community-weighted mean and variance trends will be more likely detected when weighting by abundance.

MATERIALS AND METHODS

STUDY SITES

All clearcut and fire sites used to construct chronosequences were located in and around Guánica Dry Forest in SW Puerto Rico (17$_o$58'N, 65$_o$30'W). Plots consisted of mature semi-deciduous dry tropical vegetation prior to disturbance with some variability in edaphic conditions (Appendix C). Mean annual temperature is 25.1$_o$C and mean annual precipitation is 860 mm most of which falls during a short variable spring wet season (Apr-May) and a more consistent longer hurricane season (Aug-Nov) (Murphy & Lugo, 1986b). Interannual variability in precipitation is high (Murphy & Lugo, 1986b). The natural disturbance regimes are predominantly drought and occasional hurricanes. A long legacy of anthropogenic disturbance exists among Puerto Rico's forests. Prior to protection in 1919, Guánica Forest had a history of housing, charcoal pits, cutting and grazing which has resulted in the mosaic of forests stands seen today (Molina Colon & Lugo, 2006).

Our two chronosequences differed somewhat in their construction due the availability of sites subjected to clearcutting or fire and the census history of individual sites (full details in Appendix C). Eleven clearcut communities refer to 11 individual censuses over 47 years shared between two sites ~1km apart that were cut in 1969 and 1981 respectively. Sites were cut similarly including removal of above-ground stems entirely from plots and stumps left intact. Our 10 fire communities consisted of 10 censuses over 34 years shared between four sites that burned between 1983-2012. Although one fire site is located 16km outside the forest boundary, no significant

difference in species composition or structure were found in a prior study (Allerton, 2012). Puerto Rican TDF is not considered resilient to wildfires and legacy effects (e.g. loss of canopy cover, altered understory microclimate conditions) are suspected of initiating state transitions from native forest to exotic grasslands (Van Bloem, *personal observations*).

Due to the use of historical census data to construct our chronosequences, sampling procedures were not always uniform between sites (full details Appendix C). Total area sampled in each site varied between 300-1000m^2 (0.03-0.1ha). Further, in early successional sites all woody individuals ≥0.1cm dgh were measured whereas in intermediate and later-successional sites all woody individuals ≥1cm dbh were censused. We consider these methods sufficient to accurately capture functional changes in plots because Guánica Forest is characterized by a very high density of small trees relative to other dry forests (Murphy & Lugo, 1986b) reducing the spatial coverage needed in sampling. Our chronosequences span a maximum of 47 years and thus sites likely contain few large (≥5cm) individuals. Growth rates in Puerto Rican dry forest are low (~1-2mm/ yr.) and mature forest species area curves plateau at 275-300m^2 for individuals 2.5-4.99cm dbh (Murphy & Lugo, 1986b). Biomass and species richness over the course of succession are shown in Fig 6.2.

FUNCTIONAL TRAITS

Our study evaluated the traits of 44 dry forest species important to the 'fast-slow' trait continuum and to Caribbean dry forest functioning and regeneration (Reich, 2014;

Murphy & Lugo, 1986b; Van Bloem *et al.*, 2003). As traits of cacti do not compare similarly with woody species, cacti species (specifically *Pilosocereus* and *Opuntia* sp.) were omitted from sampling. In total we collected eight leaf traits, one stem trait and one regeneration trait (Table 6.1). Although we recognize the role of ontogeny and environment in driving plastic variation among individuals, we standardized all sampling except for resprouting to adult trees from mature undisturbed forest. This way shifts in functioning among communities could more easily be attributed to the role of genetic differences among species (Kraft & Ackerly, 2014).

Standardized protocols were used in the collection of functional traits (Cornelissen *et al.*, 2003). Traits were measured on 5-10 individuals per species during the summer dry season within the insular forest and proximal to most of our sites. Upon collection, leaves were rehydrated for 24hr before scanning (Canon) and leaf area (LA, cm^2) was calculated using the software ImageJ (NIH). Fresh mass was then measured using a precision balance (±0.001) after which leaves were dried for 72hrs at 70^{o}C before recording dry mass. Specific leaf area (SLA, $cm^2\ g^{-1}$) was calculated as area/ dry mass and lead dry matter content (LDMC, $g\ g^{-1}$) as dry mass/ fresh mass. For elemental analysis, sun-exposed mature leaves from five individuals per species were dried, homogenized and ground together using a Wiley Mill to create five bulk samples per species. Samples were used to determine leaf nitrogen content (LNC, %), carbon ($\delta^{13}C$, ‰) and nitrogen ($\delta^{15}N$, ‰) isotope concentrations by Duke University's Environmental Stable Isotope Laboratory using a Carlo Erba NA 1500 Elemental Analyzer. Standardization was based on USGS-40 for $\delta^{13}C$ and Costech acetanilide for

elemental N. Additional ground leaf samples were sent to Clemson's Agricultural Service Laboratory to determine leaf phosphorus concentrations (LPC, mmol kg^{-1}) using a nitric acid- hydrogen peroxide digestion and P content determination using ICP-OES (ICP-6500 Duo, Thermo Fisher Scientific, Pittsburg, PA, USA). Wood density (WD, g cm^{-3}) was measured by taking fresh cores at dbh from five individuals per species. Fresh mass volume was recorded using the water displacement technique (Ilic *et al.*, 2000). Cores were subsequently dried for 96hr at $100^{o}C$ to ensure water had evaporated from stem cells and dry mass was recorded. WD was calculated as dry mass/ green volume. Maximum leaf water potential (Ψ_{max}, -MPa) was recorded for 3-5 individuals for all species at solar noon over consecutive days. One measurement of Ψ_{max} per tree was made using a pressure chamber (Model 1000, PMS Instrument Company, Albany OR). Where gaps existed, we supplemented missing trait values with published data from nearby sites (Sanchez *et al.*, 2015). Missing values made up for an average of 8% and 4% in clearcut and fire communities respectively (clearcut communities 0-16% and fire communities 0-24% of the total basal area).

Resprouting was captured using the species-specific annual relative growth rate (SPRT RGR, cm yr^{-1}) of the longest resprout. Resprout RGR was extrapolated based upon individual tree linear slopes analyzed using three separate census measurements taken in the months following fire and clearcut events. Sample sizes were improved by pooling and taking the average of basal collar resprouts and root suckers.

STATISTICAL ANALYSIS

We determined functional trajectories across the two chronosequences using the trait mean for all species in each community weighted by abundance or basal area (Lavorel *et al.*, 2011; Enquist *et al.*, 2015). Further, to detect mechanisms of assembly within disturbance communities, we incorporated two distinct measures of dispersion into our analysis: (i) the *range* of trait values (max-min) in order to determine whether filtering may be restricting the range of trait values compared to the regional species pool (Bernard-Vernier *et al.*, 2011) and (ii) the community-weighted variance (CWV) which allowed us to determine the shape of the trait frequency distribution within the local community structure across succession.

Within each community, the community-weighted mean (CWM) and community-weighted variance (CWV) was calculated using all species that made up 90% of the total basal area in sites (Garnier *et al.*, 2004) using the following equations:

$$\mathrm{CWM}_{jy} = \sum_{k=1}^{n_j} \mathrm{A}_{kj} z_k, \qquad \text{eqn 1}$$

$$\mathrm{CWV}_{jy} = \sum_{k=1}^{n_j} \mathrm{A}_{kj} (z_k - \mathrm{CWM}_{jy})^2, \qquad \text{eqn 2}$$

where n_j represents the total number of species sampled (and comprised 90% cumulative basal area in sites) in plot *j*, A_{kj} is the relative abundance or relative basal area of species *k* in plot *j*, and z_k is the mean trait value of species *k* (Garnier *et al.*, 2004). To identify changes in mean phenotype (CWM) and trait distributions (CWV) across our two successional gradients, we regressed the CWM and CWV values with one of two metrics

for succession depending on the weighting factor used: (i) stand age (i.e. time elapsed since disturbance) when weighted by abundance and; (ii) stand basal area when weighted by basal area. Model selection between linear and quadratic polynomial fits were determined based on the lowest AIC and highest r^2 value. The most parsimonious model was selected when lowest AIC and highest r^2 did not match.

Of significant interest was whether disturbance-types were influential in establishing the conditions that exclude particular plant strategies (i.e. trait range restriction). As such, we used a null model designed to test whether filtering was occurring within our communities based upon comparing the observed trait range (max-min) within each community with the null expectation irrespective of time since disturbance (Bernard-Verdier *et al.*, 2011). For each community, our model created a null distribution generated from 9999 random samples (without replacement) of the regional species (trait) pool, while keeping both species richness per site and species abundances within the regional pool constant (Kraft & Ackerly, 2010). To compare observed values with the null distribution, we first calculated the one-tailed probability *P* that the observed range was lower than expected (eqn 3). Then using *P*, an effect size (ES) was calculated and re-scaled by subtracting 0.5 from *P* and multiplying the result by 2 (Chase *et al.*, 2011; Bernard-Verdier *et al.*, 2012). ES values varied between -1 to 1. Negative ES values far from the null expectation (representing the median of the null distribution and marked by zero on the y-axis of Fig. 6.6 & 6.7 suggest that a smaller trait range than expected was found and thus filtering of traits. Positive ES values suggest a greater range

than expected, although this measure is sensitive to extreme values (Cornwell & Ackerly, 2009; Bernard-Verdier *et al.*, 2011).

$$P = \frac{number(null < obs) + \frac{number(null = obs)}{2}}{10000}$$

eqn 3

Two types of statistical tests on conducted on ES values. First, irrespective of time elapsed since disturbance we sought to determine patterns of community structure within our two chronosequences using a non-parametric two-sided signed-rank test (Wilcoxon's *W*) to calculate when the null and observed ES values significantly differed. Next, to test whether as succession advances, different assembly processes may be structuring clearcut and fire communities we used a non-parametric Spearman's rank-order correlation (Spearman's ρ) for ES values along succession. Significance of all analyses was performed to $\alpha = 0.05$. All analyses in this paper were conducted using R (R Core Team, 2019).

RESULTS

FUNCTIONAL TRAJECTORIES IN CLEARCUT AND FIRE SUCCESSIONAL SITES

Both clearcut and fire sites exhibited directional shifts for a number of CWM traits along succession demonstrating a gradual shift from 'slow' to 'fast' resource capture strategies. However, rates of change in CWM trait values were higher in fire relative to clearcut

sites over the course of succession (Fig. 6.3). In clearcut sites, the CWM of LA, LNC and LPC increased over time regardless of weighting factor, and the same traits showed the same trends in fire sites when weighted by abundance (Fig. 6.3, Table 6.2). Clearcut sites also exhibited a decrease in ψ_{max} (less negative) and WD when weighted by basal area and an increase in resprout RGR when weighted by abundance (Fig. 6.3, Table 6.2). SLA increased in fire sites when weighted by abundance. Basal area weighted traits demonstrated no meaningful trends in fire sites (Fig. 6.3, Table 6.2) as biomass was not found to increase logarithmically over the course of succession (Fig. 6.3).

In the PCA, both WD and ψ_{max} were important in early successional clearcut communities whereas LNC, LPC, LA, $\delta_{13}C$, $\delta_{15}N$ and SPRT RGR were grouped with later successional clearcut communities (Fig. 6.4). When weighted by abundance, early successional fire communities were well spread out across trait space but generally grouped towards WD, ψ_{max}, $\delta_{13}C$ and $\delta_{15}N$ whereas LPP, LNC, LA and SLA grouped with later successional fire communities (Fig. 6.5).

PATTERNS OF TRAIT VARIATION IN CLEARCUT AND FIRE COMMUNITIES

Based on our null model, narrower trait ranges than expected was taken as a sign of trait filtering. Based on two-sided Wilcoxon tests (*W*-stat) considering all communities collectively, clearcut sites showed little support for reductions in trait range across succession regardless of weighting factor (Fig. 6.6 & 6.7 and Appendix C). However, Spearman's correlations (ρ-stat) suggested trait ranges of $\delta_{15}N$ (both weighting factors), ψ_{max} and LDMC (weighted by basal area) were lower than expected in early succession

and greater than expected in later succession (Fig. 6.7 and Appendix C). Interestingly, there was evidence for greater ranges than expected across the whole chronosequence for traits related to water-use including ψ_{max} (weighted by abundance), $\delta_{13}C$ and WD (both weighting factors) (Fig. 6.7 & Appendix C). The same traits also showed more variable (divergent) distributions over time (Fig. 6.6 & Table 6.2). Similarly, leaf economic traits including LPC and SLA (abundance-weighted) also exhibited greater ranges than expected across succession and greater variance (divergence) over time from early to late-successional communities (Fig. 6.6 & 6.7). The range of SPRT RGR appeared to shift from lower than expected in early sites to higher than expected in older sites (Fig. 6.7) however the Spearman's correlation (ρ-stat) was not significant. Based on the CWV, clearcut communities did exhibit higher variance (divergence) in SPRT RGR values over time (Fig. 6.7).

In fire communities, only abundance-weighted traits are discussed as no meaningful trends were observed when weighting by basal area. Based on the two-sided Wilcoxon test (*W*-stat), the trait range of LA was lower than expected across succession (Fig. 6.7) indicating long-term filtering in fire communities. The Spearman's correlation (ρ-stat) however suggested the range in LA increased slightly over time (Fig. 6.7). Based on Spearman's correlations, the trait ranges of SLA and $\delta_{13}C$ were lower than expected in early succession and greater than expected in later succession, while the opposite was true for ψ_{max} and SPRT RGR (Fig. 6.6 & 6.7). The variability in SPRT RGR values also decreased (convergence) in later successional fire sites (Fig. 6.7). Refer to Table S3 for absolute trait ranges and null model output.

DISCUSSION

FUNCTIONAL RECOVERY IN CLEARCUT AND FIRE SITES

We hypothesized that we would observe contrary patterns of functional recovery among disturbance-types whereby clearcut sites would transition from 'slow' to 'fast' strategies over time, but fire sites would be dominated by 'slow' strategies over the entire successional gradient. We found mixed support for our hypothesis whereby both clearcut *and* fire sites illustrated clear shifts in function characteristic of the gradual replacement of 'slow' conservative strategies with 'fast' acquisitive strategies. Lower values of LA, LNC and LPC (both disturbance-types) and more negative ψ_{max} and higher WD (clearcut only) are indication of the 'slow' conservative resource strategies that characterize resprouting species. Resource conservation and drought tolerant are considered important traits to resprouting individuals as their drought vulnerability comes from the need to transpire water and acquire CO_2 to replace depleted carbohydrate stores and maintain growth (Eissenstat, 1997; Schwilk & Ackerly, 2005). Although smaller leaves have reduced light absorptive surface area, higher rates of convective heat loss help maintain favorable leaf temperatures and higher photosynthetic water-use efficiency in harsh early successional sites (Parkhurst & Loucks, 1972; Westoby, 2002). More negative ψ_{max} and higher WD are associated with higher resistance to hydraulic stress, longer leaf lifespan, lower rates of wet season stomatal conductance and slower overall growth (Choat *et al.*, 2006; Reich, 2014). Shifts to higher LA, ψ_{max} and lower WD over time are indication of the increased dominance of faster growing species with fast resource strategies that tend

to possess alternative mechanisms of survival under drought stress other than structural resistance (e.g. tighter control of gas-exchange to maintain more stable ψ_{max}). Early successional vegetation in clearcut plots had lower LNC despite our TDF not being N-limited (Murphy & Lugo, 1986b). This may be partly explained by the domination of non-N-fixers immediately after cutting due to asexual reproduction via resprouting. Other explanations may include: (i) inhibition of major circulation pathways of N by clearing of clearcut detritus from sites and; (ii) lower saprotroph activity as C-supplies are depleted from reduced literfall (Keenan & Kimmins, 1993). The shift over time to vegetation with greater LPC and LNC may indicate shifts towards more efficient nutrient-retention strategies, higher site net primary productivity or the greater influence of vesicular-arbuscular mycorrhizae (VAM) associations, all typical of mature forests (Murphy, 1975; Janos, 1980; Murphy & Lugo, 1986b). The arrival of the introduced N-fixing legume *Leucaena leucocephala* presumably from nearby populations was also likely influential in increasing foliar nutrients. The gradual increase in SPRT RGR underlines the shifting influence as 'shrubby' early colonizers that establish primarily from seed (e.g. *Croton* and *Lantana* spp.) are thinned out and replaced by mature tree species with stronger resprouting syndromes.

Fire sites displayed a markedly greater rate of change from 'slow' to 'fast' trait strategies relative to clearcut sites, despite the shorter chronosequence (Fig. 6.3) suggesting a more dramatic change in species composition following fire. Sharp increases in SLA, LA, LNC and LPC in later successional fire sites indicate a possible failure of many 'slow' strategy individuals to survive and a pronounced change in mean functional

strategy towards resource acquisition (Reich, 2014). Characteristic species in older burn communities include *L. leucocephala* and *Bursera simaruba*, deciduous trees that specialize in opportunistic resource uptake during favorable precipitation periods and use drought-avoidant strategies (e.g. tight stomatal control, compound leaves) to balance intense drought with fast growth (Poorter & Markesteijn, 2008). The increases in foliar N and P in older fire sites are likely linked to the abrupt change in species composition as 'fast' strategies demand higher N and P to drive photosynthesis (Reich, 2014). Also, worth consideration is the ability of the N-fixer *L. leucocephala* to enhance soil N availability as well as the increased rates of N and P flux associated with the high turnover of non-native grasses that are abundant in some of our older fire sites located nearby roads (Ehrenfeld, 2003; Chapuis-Lardy *et al.*, 2006). Overall, our results from clearcut sites were more representative than fire sites of TDF successional communities located in mainland Neotropical regions following long-term agricultural land-use (Lebrija-Trejos *et al.*, 2010; Becknell & Powers, 2014; Buzzard *et al.*, 2016). Functional recovery in clearcut sites relative to fire sites more closely resembles natural successional trajectories (e.g. see Jimenez-Rodríguez *et al.*, 2018) whereby positive shifts in resource availability ensure a gradual change in trait composition as high resprout survivorship is balanced with entry of seed dispersed individuals.

ASSEMBLY PROCESSES IN CLEARCUT AND FIRE SITES

Results support our hypothesis that contrasting sets of mechanisms are guiding assembly within Puerto Rican TDF following clearcutting and fire. However, inferred processes

were dependent on particular traits illustrating the influence of distinct filters on the different dimensions of plant strategies (Bernard-Verdier *et al.*, 2011). The contrasting patterns between clearcut and fire communities in SPRT RGR range and variance illustrated the effect disturbance filters imposed on regeneration strategies (Fig. 6.7). Reduced trait range of resprout RGR in early-successional clearcut sites may be tied to the practice of complete stem removal thereby reducing resprouting to those species with available buds close to the ground or from root stocks and with sufficient non-structural carbohydrate storage below-ground (Poorter & Kitajima, 2007; Mostacedo *et al.*, 2009). By contrast, wildfires are inherently patchy in their effects on biomass and therefore can allow for a greater range and distribution of resprouting niches to respond (Fig. 6.7) (Vesk & Westoby, 2004; Clarke, 2013).

Both clearcut and fire communities showed evidence of abiotic and biotic filtering processes, lending support that multiple assembly processes may be operating simultaneously to structure plant communities (Spasojevic & Suding, 2012). Across the chronosequence, clearcut communities showed evidence of higher than expected ranges for abundance weighted water-use and resource-acquisition traits (Fig. 6.6; ψ_{max}, $\delta_{13}C$, WD and LPC). Considering resprouting is widespread among species in this TDF, a diverse range of water-use strategies is to be expected in early successional communities reflecting ranges in undisturbed forest. Furthermore, assembly processes that structure older TDF sites including niche partitioning continue to play a role as preserved, well-established root systems remnant from pre-clearcutting enable vertical partitioning of below-ground resources (Grime, 2006; Mayfield & Levine, 2010). That said, early

clearcut sites also showed lower ψ_{max} variability (convergence) (Fig. 6.6) and when weighted by basal area, the range of ψ_{max} was also low (Appendix D). Therefore, despite a high range in drought-tolerances at the abundance level, communities at the basal-area level still tended to be functional similar and larger drought tolerant individuals dominated. In this respect, abiotic constraints likely determine the relative contribution of species within the community as early successional growth and survival rates are higher for drought tolerant species capable of maintaining resource capture in harsh conditions (Schwilk & Ackerly, 2005). The lower variance (convergence) in other resource acquisition traits including $\delta_{13}C$, WD and LPC in early-successional clearcut communities (Fig. 6.6) further underlines the preference for functionally similar conservative resource strategies (Grime, 1977; Wright *et al.*, 2004; Chave *et al.*, 2009).

By contrast in fire sites, reduced ranges in SLA, LA and $\delta_{13}C$ were indicators that disturbance filters may have restricted early-site reestablishment to a relatively small subset of species including *Bourreria succulenta*, *Crossopetalum rhacoma and Eugenia foetida*. All three species are considered excellent basal or below-ground resprouters (Allerton & Van Bloem, *personal observations*), although on closer inspection different species dominated at different early fire sites suggesting that differences in site ecology or fire-specific effects on bud availability may determine which species reestablish best. Additionally, we propose abiotic filtering may inhibit the early establishment of 'shrubby' ruderal-type species that typically rely on seed germination. For example, species in the *Croton* and *Lantana* genera are 'fast' resource strategists that were found in early clearcut communities. Physical conditions at the soil surface will differ greatly

between post-clearcut and post-fire environments, possibly affecting seed germination rates. Inhibiting factors in fire sites may include: (i) higher temperatures and lower humidity at the soil surface in fire sites due to the loss of insulating leaf litter (Eriksson *et al.,* 2003, cf. Marod *et al.,* 2001); (ii) post-fire reductions in soil nutrient availability due to volatilization and subsequent leaching (Verma *et al.,* 2019); (iii) fire damage to dormant seed banks which are already small in size with low viability and longevity (Castilleja, 1991). Root systems would have been largely preserved after fire similar to clearcutting and therefore the larger than expected range in ψ_{max} in early fire sites is likely a signal that below-ground partitioning of water acquisition similar to undisturbed forests largely persists. Therefore, both clearcut and fire sites support the presence of resource partitioning in stressful, unproductive habitats (Tilman, 1982).

Despite some similarities in the structuring of early-successional sites, trait patterns in later successional communities demonstrated two highly contrasting assembly trajectories in post-clearcut and post-fire succession. Divergence in resprout RGR in later succession clearcut communities (Fig. 6.7) suggested a temporal partitioning of regeneration strategies (Grime, 2001; Pakeman & Eastwood, 2013). Canopy cover development and higher litterfall enhances understory physical conditions, increasing rates of seed germination and entry of 'non-sprouters' and is considered a general pattern of dry forest structuring (McLaren & McDonald, 2003b; Vieira & Scariot, 2006b). Further, the improvement in site resource availability and productivity likely explains the increase in variance of water-use and nutrient acquisition traits (Fig. 6.6 & 6.7) in older clearcut sites as coexistence is driven by limited similarities in resource use among co-

occurring species (Wilson, 2007; Mayfield & Levine, 2010). In sharp contrast to clearcut sites, a marked shift towards reduced ranges and less variance (convergence) in resprout RGR in older fire communities (Fig. 6.7) are indication of an abrupt transition in species composition and filtering of all but the 'strongest' resprouters. We propose an increase in the strength of the abiotic filter linked to ongoing fire legacy effects occurs in the initial years post-fire. These abiotic constraints include lack of canopy development and drier, less humid soil conditions increase rates of resprout mortality and alter the assembly trajectory by opening up 'transient' sites to invasion by exotic C_4 grasses that are present within the regional species pool (e.g. *Megathyrsus maximus* (Jacq.) and *Cenchrus ciliaris* (L.)). This is particularly true in fire sites close to roads that are highly susceptible to grass invasion. As invasive grass dominance increases, reduced trait range of ψ_{max} and LA (Fig. 6.6 & 6.7) represent a competitive exclusion filtering hypothesis whereby strong above-ground competition for space in the dense grass cover and below-ground depletion of water by these deep rooted African grasses (Williams & Baruch, 2000) inhibit establishment of slow-growing, drought-tolerant native tree species (Violle *et al.*, 2009; Wolfe & Van Bloem, 2012). However, low density tree communities do exist in many older fire sites formed of distinct clusters of species dispersed within the 'carpets' of grass. In some sites (e.g. Cuevas, see Appendix C.1. & C.2.) these clusters are dominated by a low number of species (Fig. 6.2.) including *Bucida buceras*, *Bursera simaruba* and *Exostema caribaeum*. Interestingly, within these clusters species may partition resources over small spatial areas as demonstrated by high variances in ψ_{max}, WD, SLA and LA in fire sites 14-19 years old (Fig. 6.6 & 6.7). Facilitation may also have a role in old fire

communities as the shading and fertilization effects of the dominant but short-lived *L. leucocephala* are known to aid survival of native seedlings (Parotta, 1992; Santiago-Garcia *et al.*, 2008). These findings are noticeably different to studies in TDFs following long-term land-use changes whereby the development of competitive hierarchies or directional filtering was found to be most important in how traits structured successional processes (Lebrija-Trejos *et al.*, 2011; Alvarez-Anorve *et al.*, 2012; Buzzard *et al.*, 2016). Interestingly, our results appear to suggest assembly in high resprouting TDFs is complex as simultaneous assembly processes operate to varying degrees in both early and late successional stages following clearcut or fire.

THE USE OF WEIGHTING FACTORS TO STUDY FUNCTIONAL PATTERNS IN RESPROUTING HABITATS

We predicted that weighting by both abundance and basal area would assist in the detection of trends in clearcut sites as assembly would be driven by a diverse set of demographic forces including fast regrowth of survivors, mortality and recruitment. By contrast, a subset of slower growing resprouters and seeders would drive succession post-fire and therefore CWM and CWV trends would be more likely observed when weighting by abundance.

Despite the relatively short chronosequences we constructed, we found support for our hypothesis, with traits weighted by both abundance and basal area demonstrating trends among clearcut communities and only abundance-weighted traits were meaningfully significant in fire communities. A higher number of significant patterns

using both abundance and basal area weighting factors in clearcut sites relative to fire sites suggests greater balance between recruitment, growth and survivorship of individuals likely linked to a faster diminishment of abiotic forces (i.e. faster transition to cooler, moister conditions) that enable higher resprout survival and higher relative contribution of seedlings within communities. In general, detecting trends among abundance-weighted traits may be more successful over relatively short chronosequences, as changes in abundance can be picked up quickly - especially in regard to fast growing resprouters and ruderal-type early colonizers (e.g. *Croton* spp.) that may attain lower cut-offs in diameter measurement protocols within just a few years. The detection of fewer patterns in clearcut sites using basal area as our weighting factor may be linked to the generally low growth rate among Caribbean dry forest species (Murphy & Lugo, 1986b). That said, our study has demonstrated it possible to detect mean functional changes in successional sites when weighting by basal area in stand ages as young as 47 years old. Other dry forest studies in SW Mexico have detected functional changes in sites when weighting relative contributions of species by basal area in stands ~60 years old (Lebrija-Trejos *et al.*, 2010; Lohbeck *et al.*, 2013). Interestingly, trends in clearcut sites were still detectable despite 'bunching' of mean functional strategies in early-successional sites (Fig. 6.3), probably linked to the initial dominance of resprouting survivors. As resprouting was widespread in post-fire sites, our study was able to detect abundance-weighted trends. Ultimately, our regression approach only works when weighting by basal area if biomass increases logarithmically with time, a phenomenon we found not to be true in fire sites (Fig. 6.3) where increasingly strong abiotic forces over time appeared

to increase rates of mortality among regrowing individuals and inhibit natural trajectories of dry forest structural development.

CONCLUSION

Despite the tendency for resprouting individuals to dominate post-disturbance communities within Caribbean dry forest, our study observed directional changes in functional composition from 'slow' to 'fast' trait syndromes in secondary successional sites recovering from clearcutting and fire. Yet, marked differences in the rate of change of plant strategies between disturbance types pointed towards dissimilarities in the structuring of these respective communities. The dramatic decline of 'slow' plant strategies in fire sites likely due to high resprout mortality was in contrast to the more gradual shifts in strategies observed in clearcut sites. Despite the drought tolerance of resprouting individuals in dry forests, the strength of the abiotic filter imposed by fire legacy-effects in early-successional fire sites is an important limiting factor influencing recruitment rates and assembly mechanisms. As such, whereas clearcut communities resemble 'natural' successional trajectories, fire sites become degraded as the influence of invasive grass can introduce competitive hierarchies that inhibit further dry forest recovery. Our study highlighted how variation in resprouting niches and disturbance legacy effects on the physical environment add complexity to assembly in TDF systems by altering the balance between demographic forces structuring communities (i.e. between recruitment, growth and mortality) and enable multiple assembly processes to operate simultaneously in both early and later successional sites.

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TABLES

Table 6.1. Table of traits used in this study, their relation to plant functions and the direction of their relationship with 'fast' resource strategies (opposite direction for 'slow' strategies). '?' indicates uncertainty in regard to trait relationship with the fast-slow spectrum.

Trait	Abb.	Units	Functional significance	Direction of relationship to 'fast' strategies
Specific leaf area	SLA	$cm^2\ g^{-1}$	Photosynthesis, leaf lifespan, relative growth rate	(+)
Leaf dry matter content	LDMC	$g\ g^{-1}$	Physical resistance, stress tolerance	(-)
Leaf area	LA	cm^2	Light capture, energy balance	(+)
Leaf nitrogen content	LNC	%	Light capture, photosynthesis	(+)
Leaf phosphorus content	LPC	$mmol\ kg^{-1}$	Photosynthesis, energy transfer	(+)
Dry season maximum leaf water potential	Ψ_{max}	-MPa	Drought tolerance	(+) (less negative)
Carbon isotope composition	$\delta_{13}C$	‰	Gas exchange, water-use efficiency	(+) (less negative)
Wood density	WD	$g\ cm^{-3}$	Light capture, cavitation resistance, mechanical strength	(-)
Nitrogen isotope composition	$\delta_{15}N$	‰	Short-term N cycling	(+)?
Resprout relative growth rate	SPRT RGR	$cm\ yr^{-1}$	Reproductive strategy	(+)?

Table 6.2. Best model fits including AIC and R_2 are shown to characterize the relationship between community-weighted means (CWM) and variance (CWV) and either stand age or stand basal area as a metric for successional development in clearcut and burn sites. The CWM and CWV was calculated by weighting species for abundance or basal area. Linear (L) and quadratic (Q) models were tested. In most cases, the model with the lowest AIC and highest R_2 was selected however when these did not pair, the most parsimonious model was used (e.g. CWM LDMC weighted by relative abundance). General direction of trend is indicated. Abbreviations for traits are: specific leaf area (SLA), leaf dry matter content (LDMC), leaf area (LA), leaf nitrogen content (LNC), leaf phosphorus content (LPC), maximum leaf water potential (ψ_{max}), carbon isotope composition ($\delta_{13}C$), nitrogen isotope composition ($\delta_{15}N$), relative growth rate of longest resprout (SPRT GR) and wood density (WD). * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

	Community-weighted mean				Community-weighted variance			
	Clearcut		Fire		Clearcut		Fire	
Trait	Model	R_2 (trend)	Model	R_2 (trend)	Model	R_2 (trend)	Model	R_2 (trend)
Weighted by abundance								
SLA	Q	0.42	Q	**0.77**** **(+)**	Q	**0.54* (-)**	Q	0.27
LDMC	L	**0.65**** **(+)**	L	0.29	L	0.31	Q	0.49
LA	L	**0.46*** **(+)**	Q	**0.92***** **(+)**	L	**0.46* (+)**	Q	0.29
LNC	Q	**0.40*** **(+)**	Q	**0.69*** **(+)**	L	0.20	L	0.14
LPC	Q	**0.52**** **(+)**	Q	**0.63*** **(+)**	Q	**0.74** (+)**	L	0.30
ψ_{max}	Q	0.35	L	0.31	L	**0.70*** (+)**	L	0.19
$\delta_{13}C$	Q	0.15	L	0.17	L	**0.60** (+)**	L	0.18
$\delta_{15}N$	L	0.04	Q	0.54	Q	0.17	L	**0.52* (-)**
SPRT RGR	Q	**0.69**** **(+)**	Q	0.35	Q	**0.63* (+)**	Q	**0.59* (-)**
WD	Q	0.16	Q	0.30	L	**0.47* (+)**	Q	0.47
Weighted by basal area								
SLA	L	0.20	L	0.15	L	0.04	Q	0.44
LDMC	Q	0.21	Q	**0.40*** **(+)**	L	**0.69*** (+)**	L	0.00
LA	Q	**0.71**** **(+)**	L	0.21	L	**0.51** (+)**	Q	0.30
LNC	Q	**0.56*** **(+)**	L	0.04	L	0.33	L	0.01
LPC	Q	**0.76**** **(+)**	L	**0.42*** **(-)**	L	0.07	L	0.11
ψ_{max}	Q	**0.66**** **(-)**	L	0.30	Q	0.46	L	0.00
$\delta_{13}C$	L	0.27	L	0.13	L	0.16	L	0.01
$\delta_{15}N$	Q	0.33	Q	0.19	L	**0.44* (+)**	L	0.14
SPRT RGR	L	0.24	L	0.04	Q	0.33	L	0.11
WD	Q	**0.57*** **(-)**	L	0.11	L	**0.38* (+)**	L	0.16

FIGURES

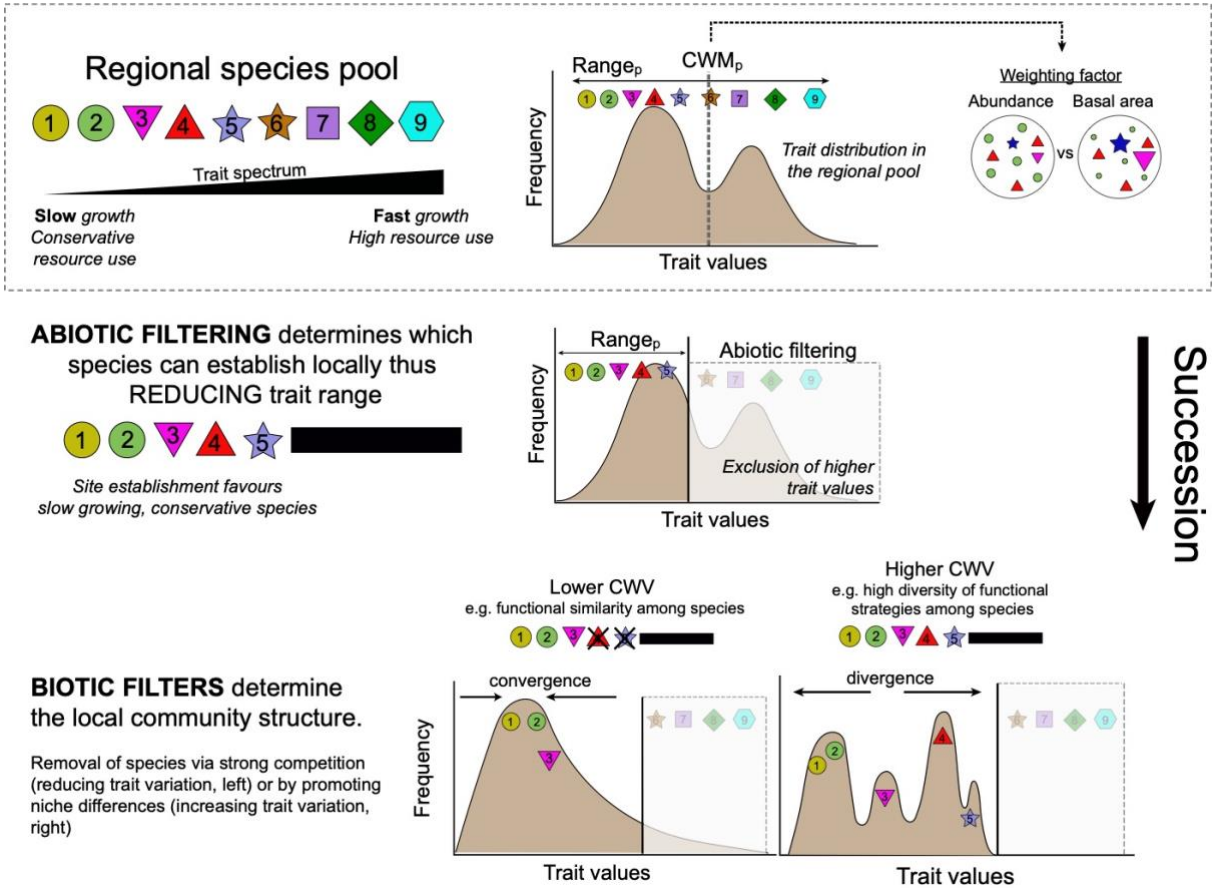


Figure 6.1. Conceptual framework for the identification of assembly mechanisms using a trait-based approach. Potential colonists (top) of a site are those species within the regional species pool. Among species, correlated traits form a fundamental spectrum of variation from 'fast' traits with high potential for resource capture to 'slow' traits that enhance water and nutrient conservation. The mean value for a given trait within a community can be determined using a weighting factor based on either species abundance or basal area. In newly disturbed sites, strong abiotic filtering is expected to limit the range of traits that are able to survive thus excluding particular species from establishing. Biotic interactions that alter community structure (i.e. the dispersion of traits) can be detected through changes in the community-weighted variance (CWV). Other potential assembly processes (e.g. facilitation, stochasticity) are not shown. Figure abbreviations include: Community-weighted mean, CWM; community-weighted variance, CWV. Adapted from Bernard-Verdier *et al.* (2012) and Woodward & Diament (1991).

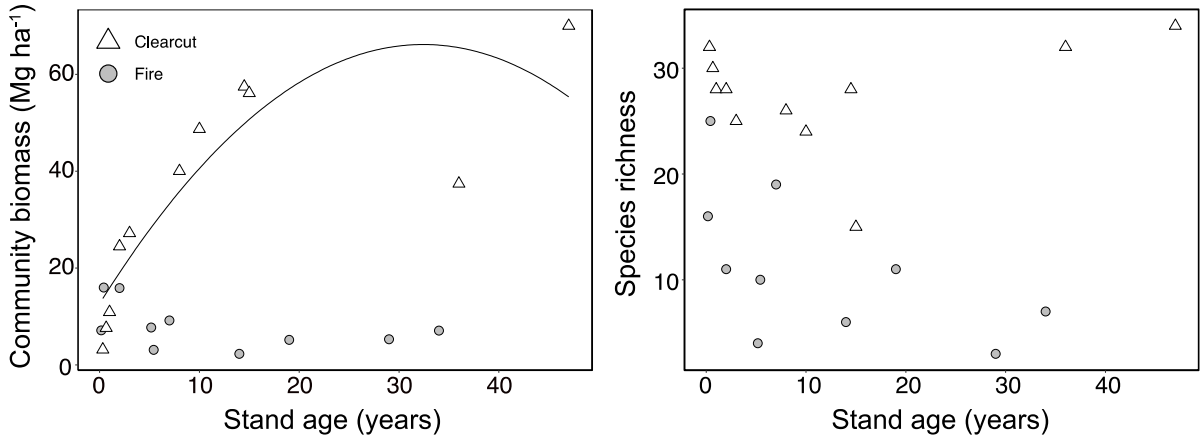


Figure 6.2. Community biomass (left) and species richness (right) over time in clearcut and fire sites. Biomass across our clearcut chronosequence followed a positive trend with succession whereas biomass in fire communities stagnated. Species richness remained high in clearcut communities but declined over time in fire communities.

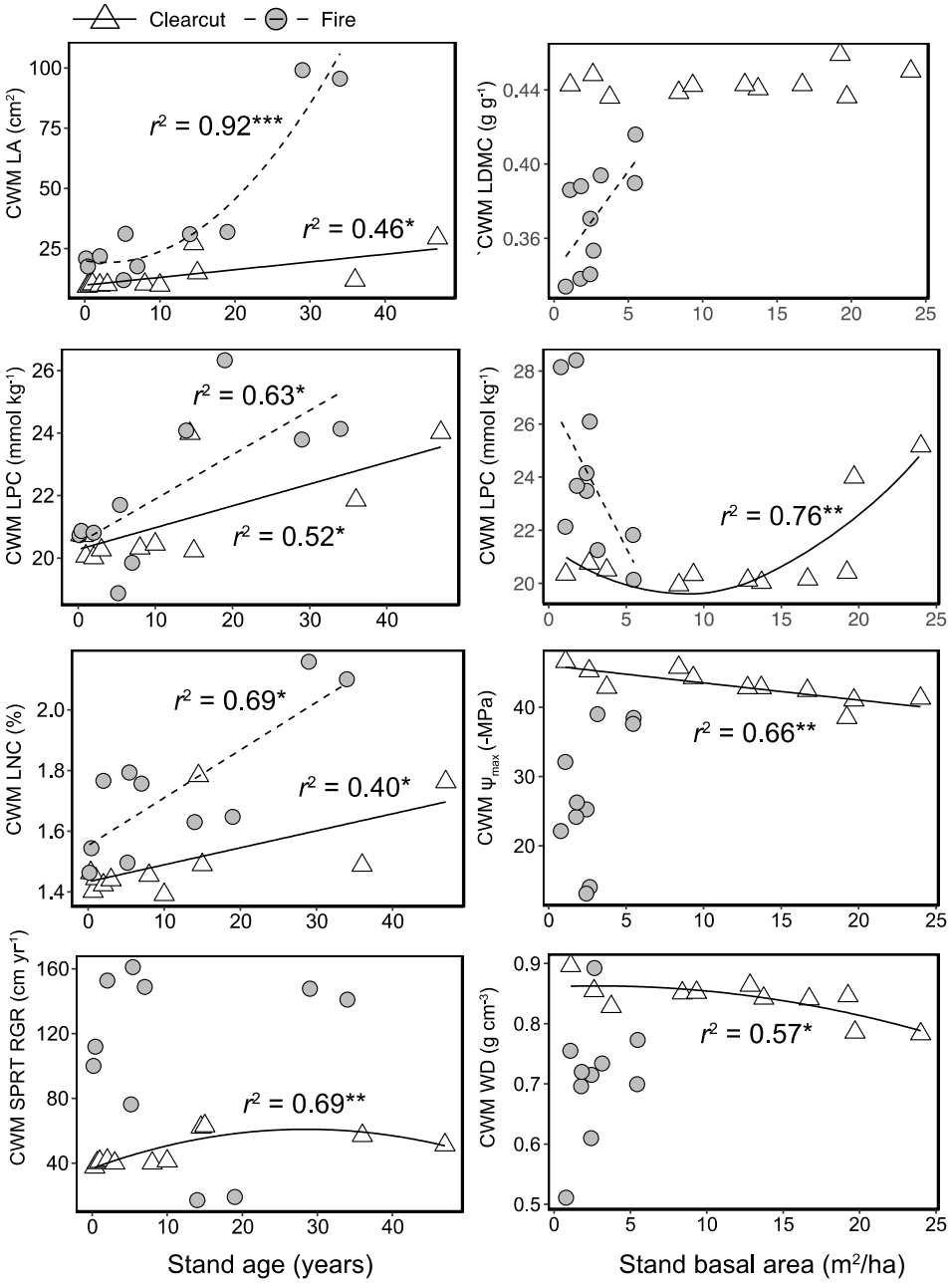


Figure 6.3. Regression trends in the community weighted mean (CWM) along the successional gradient for six traits in clearcut (open triangles and solid lines, $N = 10$) and fire (shaded circles and dashed lines, $N = 11$) chronosequences. CWM values regressed against stand age are weighted by species abundance whereas CWM values regressed against stand basal area are weighted by basal area. Abbreviations are: leaf area, LA; leaf phosphorus content, LPC; leaf dry matter content, LDMC; leaf nitrogen content, LNC; resprout relative growth rate, SPRT RGR; maximum leaf water potential, ψ_{max}; wood density, WD.

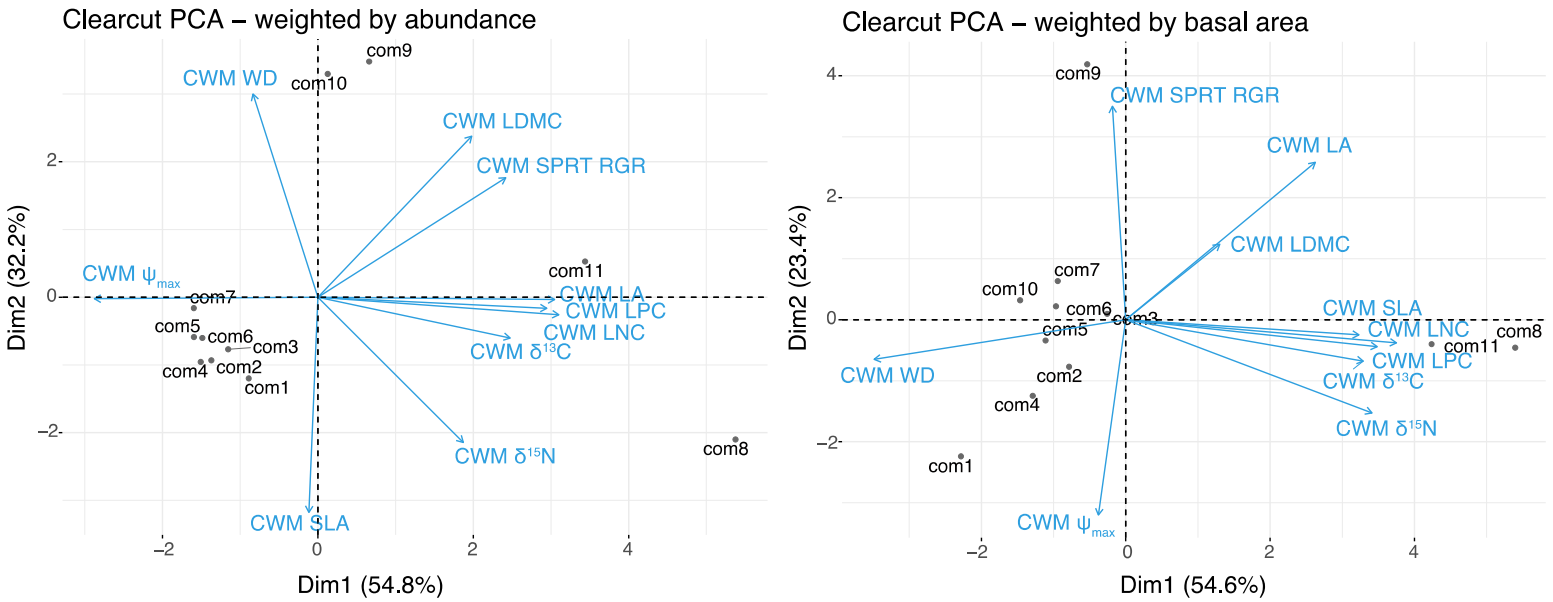


Figure 6.4. PCA trait loadings for the community-weighted mean (CWM) of traits in clearcut sites. Traits weighted by species abundance are left, and by basal area are right. Com1–11 represent 11 successional communities recovering from clearcut and in numerical order of stand age (11 being the oldest). CWM trait abbreviations include specific leaf area (SLA), leaf dry matter content (LDMC), leaf area (LA), leaf nitrogen content (LNC), leaf phosphorus content (LPC), wood density (WD), maximum leaf water potential (ψ_{max}), carbon isotope composition ($\delta_{13}C$), nitrogen isotope composition ($\delta_{15}N$), resprout growth rate (SPRT RGR).

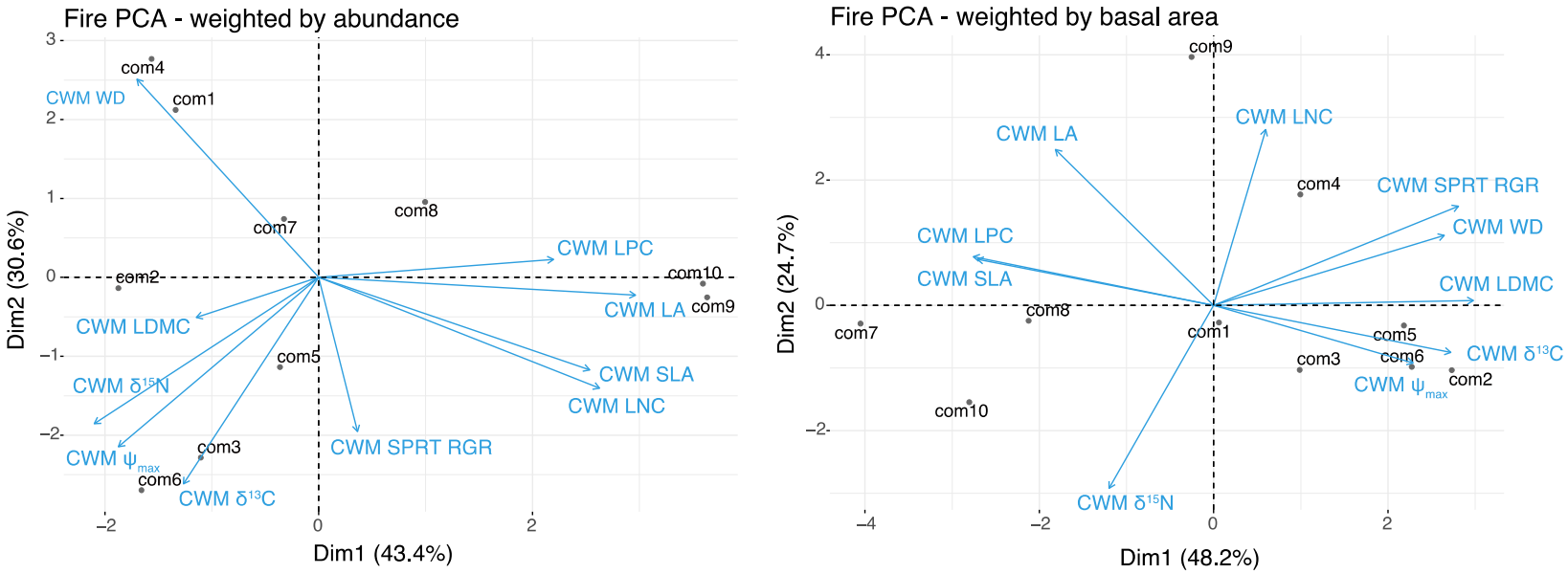


Figure 6.5. PCA trait loadings for the community-weighted mean (CWM) of traits in fire sites. Traits weighted by species abundance are left, and by basal area are right. Com1–10 represent 10 successional communities recovering from fire and in numerical order of stand age (10 being the oldest). CWM trait abbreviations include specific leaf area (SLA), leaf dry matter content (LDMC), leaf area (LA), leaf nitrogen content (LNC), leaf phosphorus content (LPC), wood density (WD), maximum leaf water potential (ψ_{max}), carbon isotope composition ($\delta_{13}C$), nitrogen isotope composition ($\delta_{15}N$), resprout growth rate (SPRT RGR).

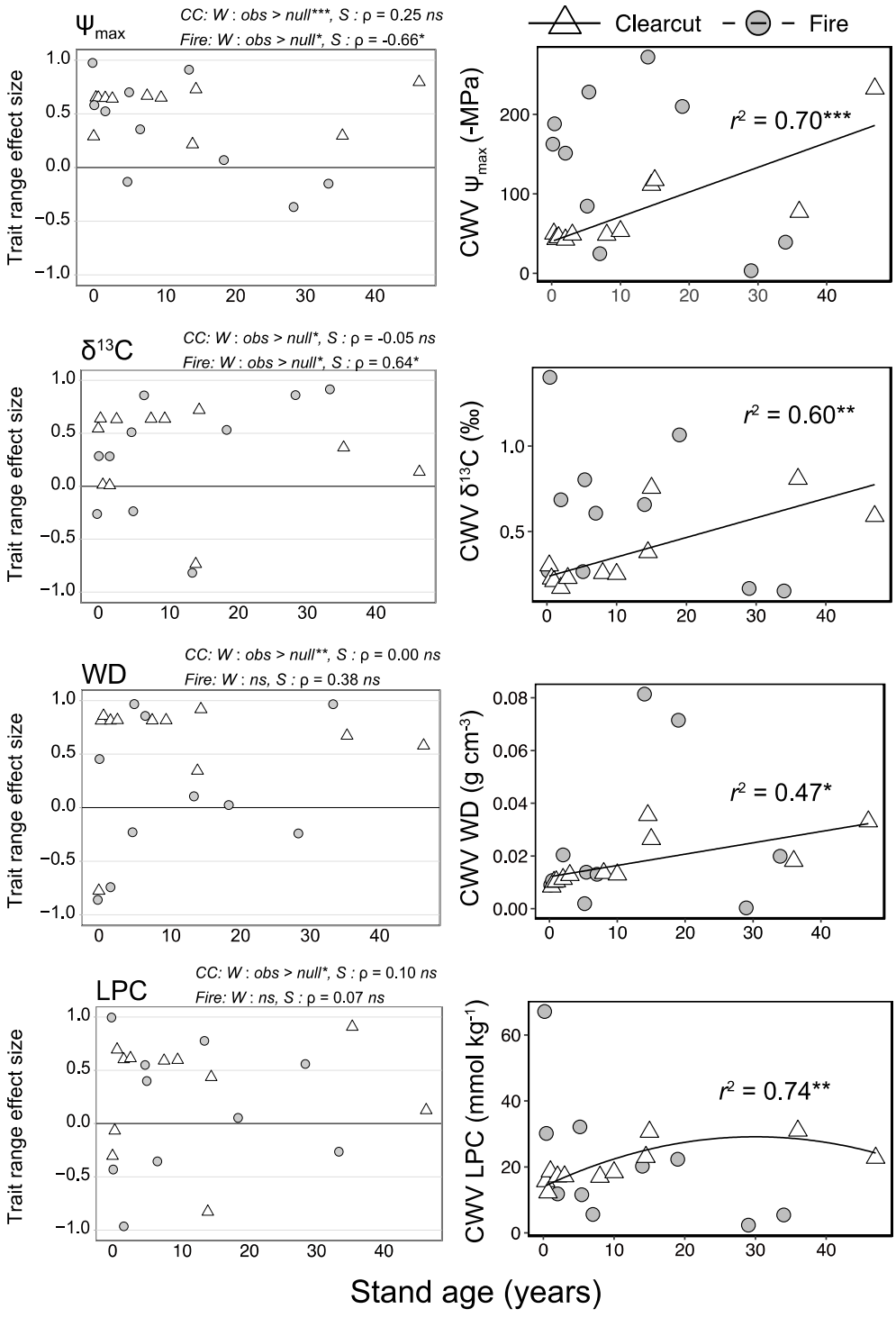


Figure 6.6. Trait dispersion along the successional gradient in clearcut (open triangles) and fire (shaded circles) communities (weighted by abundance). Left plots show community trait range variation relative to a null model of random assembly. Negative effect sizes are evidence of trait range reduction. Two-sided Wilcoxon tests (*W*) and Spearman's rank correlations (*S*) are labelled above panels. Right plots show community-weighted variance (CWV) as a function of stand age. Regression lines (continuous for clearcut sites, open for fire sites) and significant coefficients of determination (r_2) are given. Abbreviations are ψ_{max}, maximum leaf water potential; $\delta_{13}C$, carbon-isotope composition; WD, wood density; LPC, leaf phosphorus content.

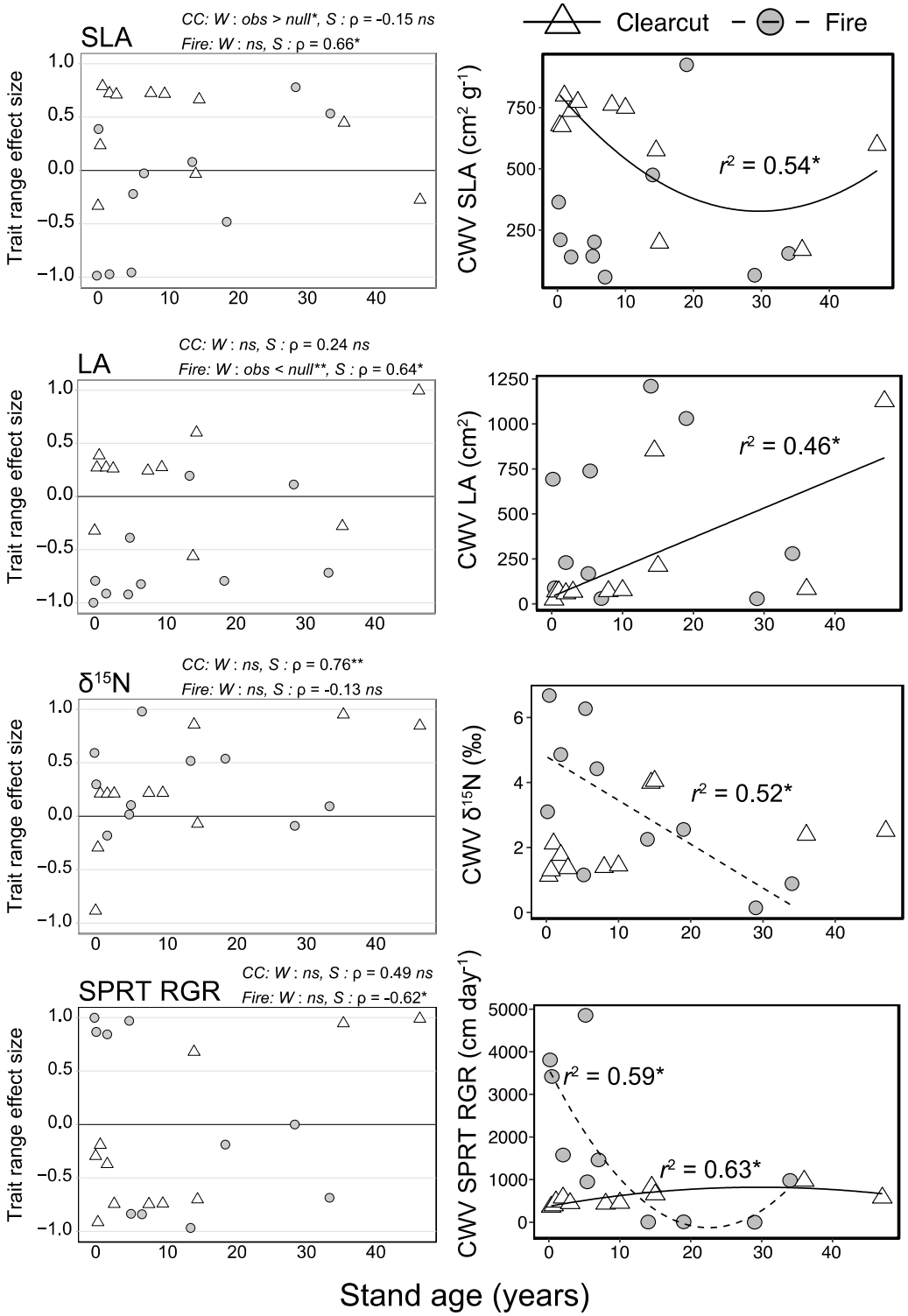


Figure 6.7. Trait dispersion along the successional gradient in clearcut (open triangles) and fire (shaded circles) communities (weighted by abundance). Left plots show community trait range variation relative to a null model of random assembly. Negative effect sizes are evidence of trait range reduction. Two-sided Wilcoxon tests (*W*) and Spearman's rank correlations (*S*) are labelled above panels. Right plots show community-weighted variance (CWV) as a function of stand age. Regression lines (continuous for clearcut sites, dashed for fire sites) and significant coefficients of determination (r_2) are given. Abbreviations are SLA, specific leaf area; LA, leaf area; δ_{15}N, nitrogen isotope composition; SPRT RGR, resprout relative growth rate (longest stem).

CHAPTER SEVEN

CONCLUDING THOUGHTS, IMPLICATIONS AND FUTURE DIRECTIONS

Until recently, plant demographic research largely focused on 'recruitment' to the neglect of 'persistence' in natural systems. Increasingly however, the role of resprouting is being viewed as a central underpinning to the persistence niche, with many studies now incorporating this functional trait into their measurements of forest recovery. This study set out to better understanding the functional attributes that drive resprouting and recovery in Puerto Rican tropical dry forest following both natural and human-caused disturbance. Research questions were framed in the context of a conceptual framework (Fig. 2.1) that outlined gaps in our understanding of the mechanisms behind TDF resprouting responses specifically in relation to buds, their protection and resourcing mechanisms.

From individuals to communities, persistence is implicit to the act of resprouting however, findings from this dissertation research illustrate that within Puerto Rican tropical dry forest persistence is highly dependent on species identity, life-history strategy and disturbance. For most of the year, water is scarce and widespread resprouting within this TDF community is likely a survival adaptation selected for in light of the physical restraints on seedling establishment and overall productivity. Resprouting was found to occur across a broad spectrum of resource capture and water-use behaviors suggesting alternative mechanisms may be more important in determining basal or underground bud banks. Nevertheless, the overall dominance of slow-growing, drought tolerant species with slower resprouting syndromes illustrates the importance of investing in tissue

structures in order to withstand the impacts of drought and maximize chances of successful reestablishment. The greater apparent success of this resprouting strategy is also likely tied to maintaining moderate resource acquisition rates during drought, as opposed to fast-growing species that require tight regulation of gas-exchange due to their weaker hydraulic architecture and drought vulnerability. Intuitively, persistence should be associated with minimizing the path to recruitment through fast growth in order to quickly exit vulnerable life stages however in this TDF, the equalizing force of the abiotic environment is such that 'playing the long game' is the only option for most species. It's noticeable that some of the 'fastest' resprouting species have unique resource-capture adaptations that provide significant advantages in terms of productivity including photosynthetic stems (*B. simaruba*), nitrogen fixation (*L. leucocephala*) and ectomycorrhizal fungi (*Coccoloba* spp.).

Ultimately though, disturbance-type and intensity are hugely important in determining successful recovery of TDF because individuals and communities rely heavily on the persistence of above-ground structures. This was well demonstrated by the leaf-level plastic responses that were observed in response to Hurricane Maria and provide an insight into the variety of resilience mechanisms these systems possess. These significant gains in resource acquisition now offer an exciting avenue of research into understanding their potential to fund additional recovery structures other than leaves such as resprouting. In terms of anthropogenic disturbances, those that more closely replicate 'natural' events will reduce the strength of the abiotic filter and increase the chances of a successful return to mature forest. Small-scale clearcutting appears to be successful in

this regard whereby resprouting from preserved underground structures and lower impacts to the forest floor environment promote direct regeneration of much of the pre-disturbance community (i.e. autosuccession), increasing productivity and diversification of forest function over time. The legacy effects of fire by contrast impose long-lasting changes to the physical environment that push even strong drought tolerant resprouters beyond their physiological limits thus inducing death. The presence of species with strong resprouting syndromes, fast potential for resource capture and drought avoidance mechanisms may be key to persistence of a native tree community in fire sites because these species are more effectively able to compete with invasive grasses for space and resources. Similar functional types also have an important role to play in increasing facilitative biotic interactions through their ability to ameliorate microsite conditions. Overall, maintenance of stem and canopy structures are key to ensuring stable recovery trajectories and persistence in TDF by allowing trees to optimize their responses to disturbance, often through unexpected ways.

These findings have implications for modelling by demonstrating leaf habit as an ineffective plant functional type to aggregate disturbance responses among species within Puerto Rican tropical dry forest. That said, by considering where species were distributed along continuums of resource-use (e.g. stomatal responses) and regeneration (e.g. resprouting), this dissertation contains a significant quantity of biological information that can be directed towards quantifying the distribution of species along trade-off axes – a method that ultimately may perform better at capturing the effects of biodiversity on forest function in vegetation models. In addition, these results can inform modelling of

forest succession by illustrating the relative utility of incorporating resprouting as a regeneration mechanism among different disturbance types. To be influential, resprouting must translate into persistence however, when resprout mortality is high (as our results from fire sites implied), their importance in models diminishes.

In terms of conservation, there is a requirement to understand the consequences of plant persistence under future climate scenarios. This need became apparent during my research with the occurrence of a severe drought in 2015 and a major hurricane in 2017. In many ways these single events are representative of observed changes in climate around the world and pose questions such as how resprouters in TDFs will respond to declines in fauna, more frequent and extreme climate, greater atmospheric CO_2 concentration and the influence of invasive species. Declines in pollinators and dispersers are less likely to affect resprouters however, if drought conditions intensify resprouters will likely be at a disadvantage due to their limited ability to shift ranges. Resprouters in Puerto Rican TDF may already be living close to their physiological limits as demonstrated by the dramatic shifts in community function we observed in fire sites indicative of delayed resprout mortality from abiotic stress. More intense hurricanes may favor resprouters in Puerto Rican TDF as resprouting and its association with multiple stem growth forms has already been recognized as an adaptive response to windthrow. The short-term physiological responses we observed are further evidence of resilience to these events.

Overall, these findings extend our understanding into the breadth of persistence and regeneration mechanisms available to tropical dry forest trees and indicate these

systems can be resilient to some forms of intense human-caused disturbance. Stemming from this research are a number of questions that could form the basis of future studies into the nature of the persistence niche within TDFs:

- What is the distribution of anatomical, morphological and physiological traits of resprouts within and among species, and to what extent do they reflect adult-stage mean values and inter- and intra-specific variation?
- What are the costs associated with resprouting in a system where stem persistence is an important element to ensuring successful recovery? How is C allocated to stem vs root storage and does this impact on adult growth? How do allocation patterns relate to resprout bud locations?
- What proportion of resprouting is funded by internal stores of non-structural carbohydrates vs new assimilates acquired from the return of photosynthesis? How does this vary between species and plant functional types?
- What are the demographic implications of post-hurricane leaf plastic responses? Are potential productivity benefits to the community offset by higher rates of mortality due to lower drought tolerance in cheaper leaves? Is lower plasticity among some species associated with higher mortality the following dry season?

APPENDICES

APPENDIX A

Hydraulic properties for 31 Puerto Rican dominant tropical dry forest species

Figure A.1. Mean trait values (±SE) for 31 TDF species in Puerto Rico, including information on leaf habit and structure (number of stems). *Information on the mean number of stems was compiled from personal data together with values reported by Van Bloem et al. (2003). †g_{smax} data is from the 2017 mid-summer dry season rather than the 2017 winter dry season. Abbreviations as in Table 2.

Species	Family	Leaf habit	Mean no. stems*	ψ_{max} (-MPa)	ψ_{dv} (-MPa)	g_{smax} (mmol m^{-2} s^{-1})	$\delta_{13}C$ (-‰)	WD (g g^{-1})	SLA (cm^2 g^{-1})	LDMC (g g^{-1})	LA (cm^2)	Ds (no. mm^2)
Amyris elemifera	Rutaceae	EG	1.5	6.1 ± 0.15	2.3 ± 0.23	296 ± 32	28.2 ± 0.09	0.90 ± 0.02	75.9 ± 3.7	0.55 ± 0.02	16.94 ± 1.0	201 ± 15.1
Bourreria succulenta	Boraginaceae	SDEC	1.5	4.8 ± 0.25	1.0 ± 0.08	405 ± 38	26.1 ± 0.20	0.68 ± 0.02	103.5 ± 5.8	0.38 ± 0.02	17.21 ± 2.1	140 ± 5.0
Bucida buceras	Combretaceae	SDEC	2.3	3.9 ± 0.13	1.0 ± 0.07	329 ± 50	27.3 ± 0.31	0.87 ± 0.03	91.7 ± 5.1	0.48 ± 0.02	10.03 ± 1.5	205 ± 16.3
Bursera simaruba†	Burseraceae	DEC	1.0	0.6 ± 0.05	0.3 ± 0.06	53 ± 40	28.4 ± 0.18	0.25 ± 0.01	147.2 ± 6.6	0.28 ± 0.01	99.69 ± 9.5	329 ± 33.7
Coccoloba diversifolia	Polygonaceae	EG	3.1	3.3 ± 0.17	0.7 ± 0.29	50 ± 40	28.7 ± 0.38	0.77 ± 0.03	79.2 ± 1.6	0.46 ± 0.01	22.18 ± 1.4	128 ± 8.8
Coccoloba microstachya	Polygonaceae	SDEC	6.1	4.0 ± 0.24	1.1 ± 0.15	82 ± 10	27.3 ± 0.29	0.75 ± 0.02	83.4 ± 4.2	0.53 ± 0.03	11.56 ± 1.4	109 ± 10.3
Colubrina arboreceans	Rhamnanceae	DEC	2.4	5.1 ± 0.13	0.6 ± 0.12	227 ± 19	26.7 ± 0.60	0.91 ± 0.02	93.8 ± 3.9	0.39 ± 0.01	41.64 ± 2.6	132 ± 14.9
Comocladia dodonea	Anacardiaceae	SDEC	3.7	1.1 ± 0.04	0.1 ± 0.03	286 ± 17	27.8 ± 0.43	0.91 ± 0.03	84.0 ± 6.7	0.35 ± 0.01	33.13 ± 4.2	532 ± 74.4
Crossopetalum rhacoma	Celastraceae	SEG	2.5	3.3 ± 0.17	0.8 ± 0.08	220 ± 16	28.2 ± 0.23	0.84 ± 0.04	63.5 ± 5.8	0.41 ± 0.01	3.22 ± 0.3	178 ± 13.8
Elaeodendrum xylocarpum	Celastraceae	EG	1.6	3.6 ± 0.15	1.2 ± 0.15	224 ± 17	29.4 ± 0.22	0.73 ± 0.01	37.0 ± 4.1	0.50 ± 0.03	2.74 ± 0.6	174 ± 3.1
Erithalis fruticosa	Rubiaceae	EG	4.4	4.1 ± 0.25	1.1 ± 0.07	253 ± 43	27.3 ± 0.25	0.99 ± 0.06	54.0 ± 3.2	0.36 ± 0.01	11.63 ± 1.4	241 ± 14.5
Erithroxylon areolatum	Erythroxylaceae	DEC	1.2	5.4 ± 0.28	0.7 ± 0.13	76 ± 14	27.4 ± 0.21	0.92 ± 0.02	139.1 ± 6.1	0.37 ± 0.01	15.03 ± 1.4	NA
Erithroxylon rotundifolium	Erythroxylaceae	SDEC	2.3	5.1 ± 0.19	0.8 ± 0.10	83 ± 11	28.5 ± 0.36	0.97 ± 0.05	120.2 ± 9.7	0.42 ± 0.02	23.22 ± 1.0	180 ± 4.4
Eugenia foetida	Myrtaceae	EG	1.4	5.7 ± 0.24	2.1 ± 0.34	433 ± 29	28.6 ± 0.28	0.77 ± 0.01	81.0 ± 7.0	0.45 ± 0.02	3.37 ± 0.2	798 ± 34.4
Eugenia rhombea	Myrtaceae	EG	2.5	7.1 ± 0.04	0.7 ± 0.13	302 ± 23	28.0 ± 0.19	0.79 ± 0.01	68.4 ± 1.7	0.44 ± 0.01	4.05 ± 0.3	512 ± 16.0
Exostema caribaeum	Rubiaceae	DEC	1.2	5.0 ± 0.09	1.7 ± 0.02	358 ± 76	26.9 ± 033	0.90 ± 0.02	120.3 ± 6.0	0.38 ± 0.01	10.60 ± 0.7	278 ± 15.4
Guettarda elliptica	Rubiaceae	SDEC	6.4	5.9 ± 0.51	0.8 ± 0.07	898 ± 178	28.6 ± 0.04	0.76 ± 0.02	119.3 ± 6.0	0.44 ± 0.01	7.50 ± 1.2	137 ± 14.4
Guettarda krugii	Rubiaceae	SDEC	3.4	5.0 ± 0.39	1.0 ± 0.18	929 ± 40	28.4 ± 0.14	0.79 ± 0.05	78.7 ± 4.8	0.46 ± 0.01	23.66 ± 3.5	NA
Gymnanthes lucida	Euphorbiaceae	EG	1.5	5.8 ± 0.11	1.1 ± 0.12	168 ± 15	27.9 ± 0.31	0.96 ± 0.02	81.9 ± 4.2	0.45 ± 0.00	7.56 ± 0.9	322 ± 9.2
Jacquinia berteroi	Theophrastaceae	EG	4.1	2.9 ± 0.16	1.2 ± 0.19	332 ± 111	25.9 ± 0.34	0.71 ± 0.04	58.3 ± 4.1	0.45 ± 0.01	1.57 ± 0.1	80 ± 4.3
Krugiodendron ferreum	Rhamnaceae	EG	1.2	5.4 ± 0.16	1.4 ± 0.11	264 ± 34	28.7 ± 0.37	1.04 ± 0.05	106.6 ± 2.7	0.45 ± 0.01	7.92 ± 0.9	534 ± 27.1
Leucaena leucocephala	Fabaceae	DEC	1.3	2.6 ± 0.10	1.0 ± 0.10	669 ± 65	27.9 ± 0.34	0.72 ± 0.02	127.5 ± 3.5	0.39 ± 0.01	99.97 ± 18.0	174 ± 12.4
Mosiera xerophytica	Myrtaceae	SEG	6.4	3.8 ± 0.36	1.3 ± 0.23	358 ± 38	28.2 ± 0.27	0.89 ± 0.01	80.0 ± 4.3	0.47 ± 0.01	13.51 ± 1.4	320 ± 27.1
Pictetia aculeata	Fabaceae	DEC	2.4	3.7 ± 0.33	0.5 ± 0.08	584 ± 51	25.2 ± 0.21	1.03 ± 0.01	113.3 ± 4.9	0.47 ± 0.03	24.90 ± 1.6	184 ± 10.1
Pisonia albida	Nyctaginaceae	DEC	1.6	2.3 ± 0.07	0.5 ± 0.06	378 ± 25	27.9 ± 0.22	0.44 ± 0.01	109.8 ± 3.3	0.32 ± 0.01	22.14 ± 2.2	124 ± 2.6
Pithocellobium ungis-cati†	Fabaceae	SDEC	7.2	5.1 ± 0.06	0.9 ± 0.06	94 ± 19	27.4 ± 0.25	0.75 ± 0.03	119.1 ± 3.6	0.49 ± 002	11.82 ± 0.7	580 ± 29.1
Plumeria alba†	Apocynaceae	DEC	1.2	1.5 ± 0.04	0.1 ± 0.07	127 ± 21	25.2 ± 0.32	0.60 ± 0.02	74.4 ± 5.8	0.23 ± 0.01	64.70 ± 3.9	NA
Reynosia vivesiana	Rhamnaceae	EG	6.0	3.7 ± 0.42	1.1 ± 0.42	448 ± 51	28.3 ± 0.23	0.93 ± NA	57.8 ± 1.7	0.54 ± 0.02	13.75 ± 1.0	340 ± 22.9
Tabebuia heterophylla	Bignoniaceae	DEC	6.5	2.6 ± 0.16	0.9 ± 0.10	365 ± 48	26.5 ± 0.56	0.62 ± 0.01	77.0 ± 3.0	0.45 ± 0.02	10.80 ± 1.3	126 ± 10.2
Thouinia portoricensis†	Sapindaceae	DEC	4.2	4.5 ± 0.19	1.3 ± 0.14	92 ± 80	29.3 ± 0.43	1.17 ± 0.20	84.0 ± 2.4	0.47 ± 0.01	25.33 ± 3.2	410 ± 23.4
Zanthoxylum flavum	Rutaceae	DEC	1.5	5.0 ± 0.26	0.6 ± 0.10	190 ± 33	26.1 ± 0.34	0.84 ± 0.02	81.1 ± 3.5	0.39 ± 0.01	117.9 ± 17.5	142 ± 10.8

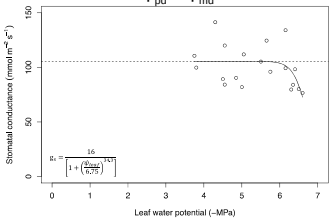
APPENDIX B

Regression curves for the response of stomatal conductance (g_s) to leaf water potential (ψ_l) for 31 Puerto Rican dominant tropical dry forest species

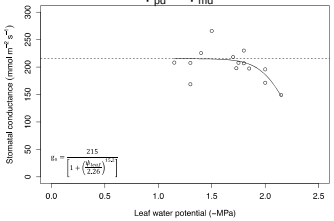
Figure B.1. Full set of regression curves of the response of stomatal conductance (g_s) to leaf water potential (ψ_l) for all 31 TDF species, grouped by leaf habit and anisohydric/ isohydric classification from our ψ_{pd} x ψ_{md} linear mixed model including slope (σ) coefficients. Regression curves are based on spring 2017 dry season data. Linear mixed model classifications and coefficients (above curves) are from summer 2016 dry season data. Species-specific regression curve equations are included. Dashed horizontal lines represent the fitted maximum for g_s. Scales are not standardized across plots in order to improve resolution.

Deciduous
Extreme anisohy.

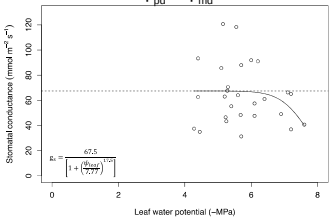
Thouinia portoricensis
Summer 16 ψ_{pd} x ψ_{md} σ = 1.15



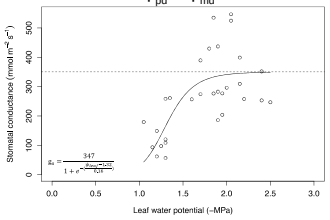
Colubrina arboreceans
Summer 16 ψ_{pd} x ψ_{md} σ = 0.95



Erithroxylum areolatum
Summer 16 ψ_{pd} x ψ_{md} σ = 0.96

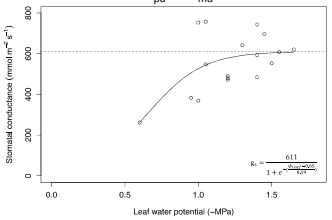


Exostema caribaeum
Summer 16 ψ_{pd} x ψ_{md} σ = 1.06

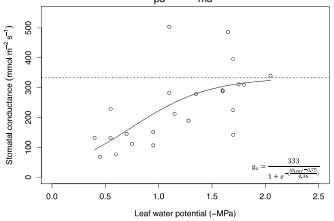


Deciduous
Strict anisohy.

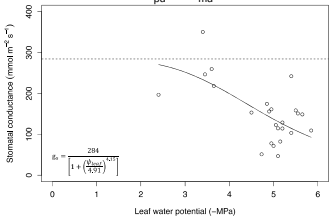
Leucaena leucocephala
Summer 16 ψ_{pd} x ψ_{md} σ = 1.08



Tabebuia heterophylla
Summer 16 ψ_{pd} x ψ_{md} σ = 1.03

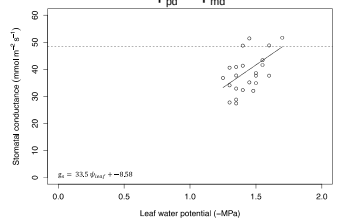


Zanthoxylum flavum
Summer 16 ψ_{pd} x ψ_{md} σ = 0.94

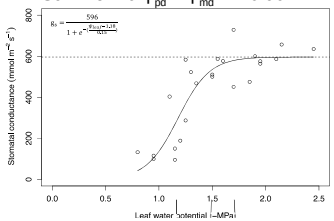


Deciduous
Partial isohydric

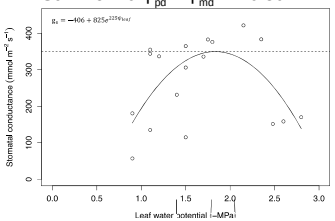
Bursera simaruba
Summer 16 ψ_{pd} x ψ_{md} σ = 0.35



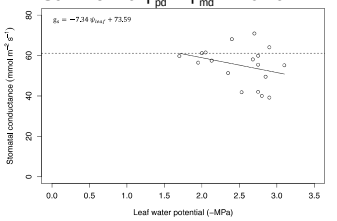
Pictetia aculeata
Summer 16 ψ_{pd} x ψ_{md} σ = 0.90



Pisonia albida
Summer 16 ψ_{pd} x ψ_{md} σ = 0.80

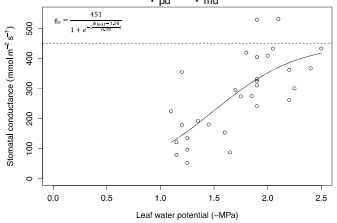


Plumeria alba
Summer 16 ψ_{pd} x ψ_{md} σ = 0.49

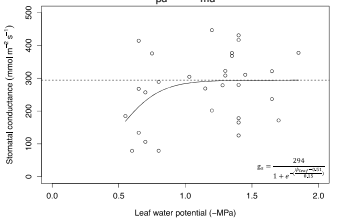


Semi-deciduous
Partial isohydric

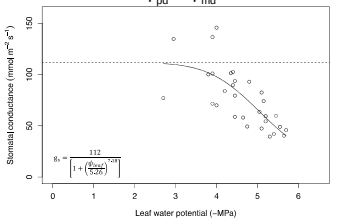
Bourreria succulenta
Summer 16 ψ_{pd} x ψ_{md} σ = 0.88



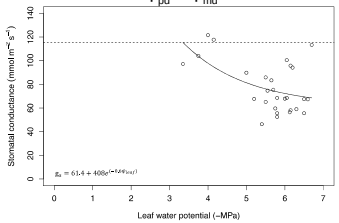
Bucida buceras
Summer 16 ψ_{pd} x ψ_{md} σ = 0.85



Coccoloba microstachya
Summer 16 ψ_{pd} x ψ_{md} σ = 0.86

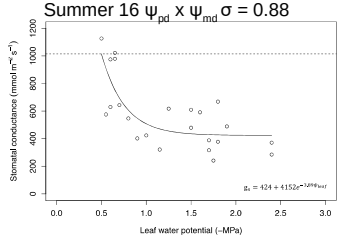


Erithroxylum rotundifolium
Summer 16 ψ_{pd} x ψ_{md} σ = 0.85

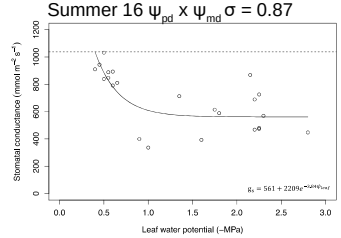


Semi-deciduous
Partial isohydric

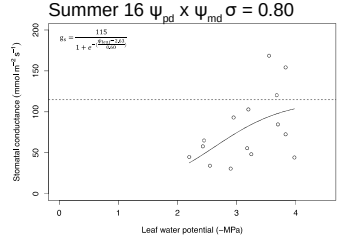
Guettarda elliptica
Summer 16 ψ_{pd} x ψ_{md} σ = 0.88



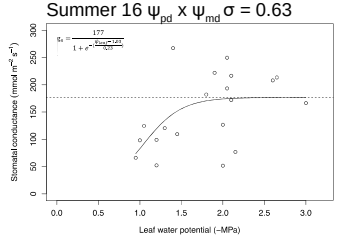
Guettarda krugii
Summer 16 ψ_{pd} x ψ_{md} σ = 0.87



Pithecellobium ungis-cati
Summer 16 ψ_{pd} x ψ_{md} σ = 0.80

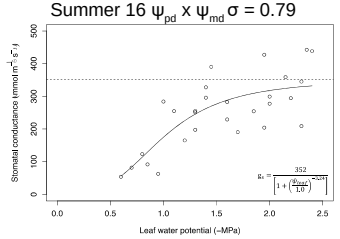


Crossopetalum rhacoma
Summer 16 ψ_{pd} x ψ_{md} σ = 0.63



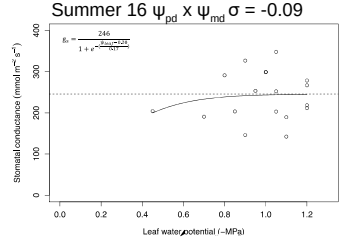
Semi-deciduous
Partial isohydric

Mosiera xerophytica
Summer 16 ψ_{pd} x ψ_{md} σ = 0.79



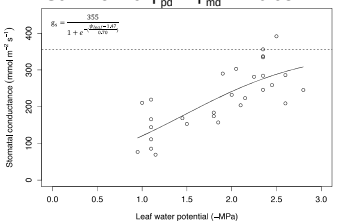
Semi-deciduous
Strict isohydric

Comocladia dodonea
Summer 16 ψ_{pd} x ψ_{md} σ = -0.09



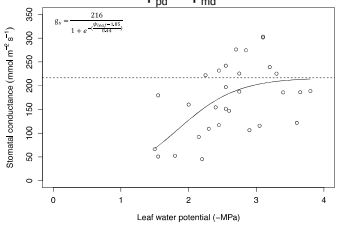
Evergreen
Strict anisohy.

Amyris elemifera
Summer 16 ψ_{pd} x ψ_{md} σ = 0.93

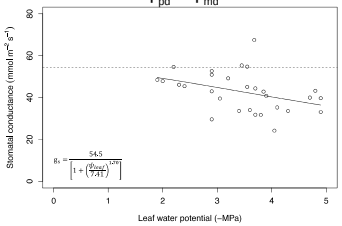


Evergreen
Partial isohydric

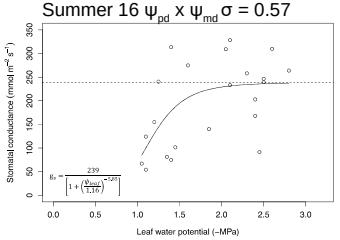
Elaeodendrum xylocarpa
Summer 16 ψ_{pd} x ψ_{md} σ = 0.49



Coccoloba diversifolia
Summer 16 ψ_{pd} x ψ_{md} σ = 0.33

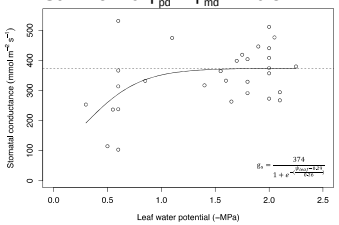


Erithalis fruticosa
Summer 16 ψ_{pd} x ψ_{md} σ = 0.57

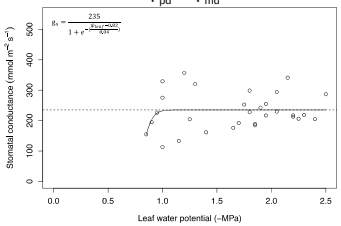


Evergreen
Partial isohydric

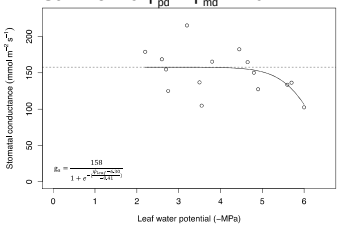
Eugenia foetida
Summer 16 ψ_{pd} x ψ_{md} σ = 0.87



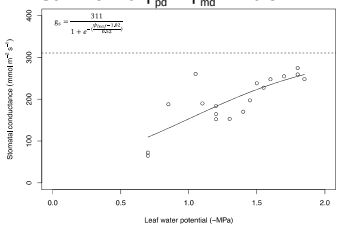
Eugenia rhombea
Summer 16 ψ_{pd} x ψ_{md} σ = 0.72



Gymnanthes lucida
Summer 16 ψ_{pd} x ψ_{md} σ = 0.71

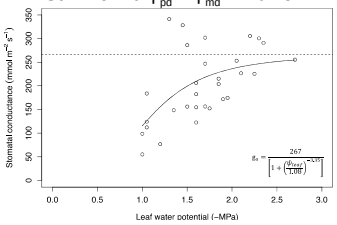


Jacquina berteroi
Summer 16 ψ_{pd} x ψ_{md} σ = 0.31

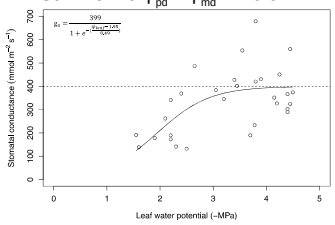


Evergreen
Partial isohydric

Krugiodendron ferreum
Summer 16 ψ_{pd} x ψ_{md} σ = 0.73



Reynosia vivesiana
Summer 16 ψ_{pd} x ψ_{md} σ = 0.62



APPENDIX C

Sampling and ecological characteristics of communities used to construct fire and clearcut chronosequences.

Table C.1. Sampling and ecological characteristics of clearcut communities

Com	Site ID	Census date (MM/YYYY)	Time since fire/ cutting	Area sampled (ha)	A. Total species present (no cacti)	B. Total species equal to 90% stand BA (B/A)	Percent total species based on tree density	Site-specific ecological characteristics and past land-use history
Clearcut communities								
1	Murphy & Lugo	11/1981	4mo	0.05	32	13 (41%)	81%	Com 1-7: Insular Guánica Forest site. Mollisol with shallow dark brown clay loam or clay surface horizon. 23-30% organic matter content. Exposed limestone rock a surface phenomenon. Roots penetrate soft limestone easily.
2	Murphy & Lugo	03/1982	8mo	0.05	30	12 (40%)	84%	
3	Murphy & Lugo	08/1982	13mo	0.05	28	13 (46%)	78%	
4	Murphy & Lugo	06/1983	2yr	0.05	28	11 (39%)	77%	
5	Murphy & Lugo	06/1984	3yr	0.05	25	11 (44%)	76%	
6	Murphy & Lugo	11/1989	8.5yr	0.05	26	11 (42%)	80%	
7	Murphy & Lugo	12/1991	10.5yr	0.05	24	11 (46%)	82%	
8	Ewel	03/1982	13yr	0.02	28	17 (61%)	93%	Insular Guánica Forest site. Mollisol with shallow dark brown clay loam or clay surface horizon. 23-30% organic matter content. Exposed limestone rock a surface phenomenon. Roots penetrate soft limestone easily. Free from grazing and fire for ~40 years but had been subjected to some cutting.
9	Murphy & Lugo	02/1996	14.5yr	0.05	15	8 (53%)	73%	See Com 1-7
10	Murphy & Lugo	07/2016	35yr	0.05	32	15 (47%)	87%	
11	Ewel	07/2016	47yr	0.10	34	14 (41%)	76%	See Com 8

Table C.2. Sampling and ecological characteristics of fire communities

Com	Site ID	Census date (MM/YYYY)	Time since fire/ cutting	Area sampled (ha)	A. Total species present (no cacti)	B. Total species equal to 90% stand BA (B/A)	Percent total species based on tree density	Site-specific ecological characteristics and past land-use history
Fire communities								
1	Tallaboa	06/2012	2mo	0.06	16	9 (56%)	83%	Only site outside Guánica Forest approximately 8km east. Steep seaward facing slopes with high exposure. Mollisols with stony-clay loam. A previous burn in 1992 overlapped much of the same area.
2	Ensenada A	06/2012	5mo	0.06	25	11 (44%)	79%	Insular Guánica Forest patch on a high ridge with moderate exposure. Entisols with shallow clayey-skeletal soils. Undisturbed since pre-1930.
3	Ensenada B	06/2012	2yr	0.03	11	9 (82%)	97%	Fire occurred adjacent to Ensenada A site. Entisols with shallow clayey-skeletal soils. Undisturbed since pre-1930.
4	Tallaboa	11/2017	5yr	0.06	4	2 (50%)	96%	See Comm 1.
5	Ensenada A	07/2017	5yr	0.06	10	6 (60%)	75%	See Comm 2.
6	Ensenada B	07/2017	7yr	0.06	19	7 (37%)	84%	See Comm 3.
7	Cuevas	06/2012	14yr	0.03	6 (1)	5 (83%)	70%	Com 7-8: Patchy scrub dry forest vegetation with rocky outcrops. Shallow, red friable limestone soils with shallow soil depths and low infiltration rates. Cactus *Pilosocereus royenii* dominant in basal area but low in abundance - excluded from analysis. Trees include *Bucida buceras*, *Bursera simaruba* and *Exostema caribaeum*.
8	Cuevas	07/2017	19yr	0.05	11 (1)	8 (73%)	73%	
9	Las Latas	06/2012	29yr	0.03	3 (1)	2 (67%)	88%	Com 9-10: In area of abandoned cornfields (abandoned in 1950's) though aerial photos from 1930 show plot sites as forested. Patchy scrub dry forest vegetation with rocky outcrops. Shallow, red friable limestone soils with shallow soil depths and low infiltration rates. Dominated by *L. leucocephala*.
10	Las Latas	07/2017	34yr	0.05	7 (1)	5 (71%)	93%	

APPENDIX D

Community trait range variation relative to null models of random assembly for communities weighted by abundance and basal area.

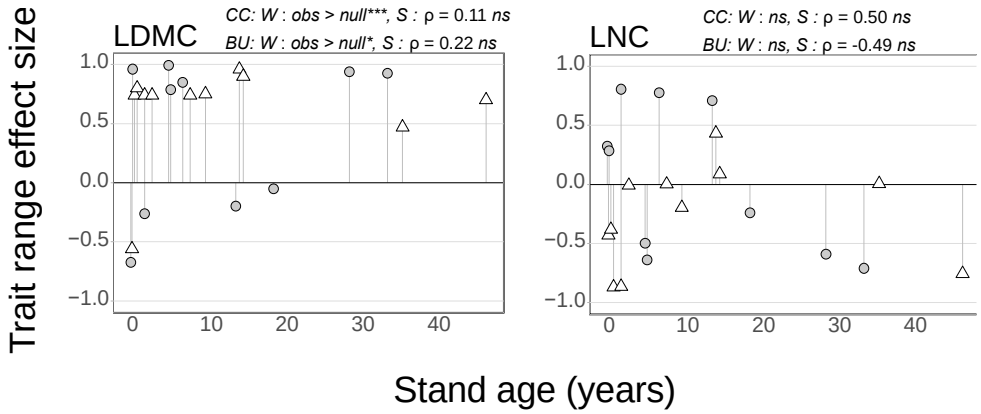


Figure D.1. Trait dispersion along the successional gradient in clearcut (open triangles) and fire (shaded circles) communities (weighted by abundance). Plots show community trait range variation relative to a null model of random assembly. Negative effect sizes are evidence of trait range reduction. Two-sided Wilcoxon tests (*W*) and Spearman's rank correlations (*S*) are labelled above panels. Abbreviations are LDMC, leaf dry matter content; LNC, leaf nitrogen content.

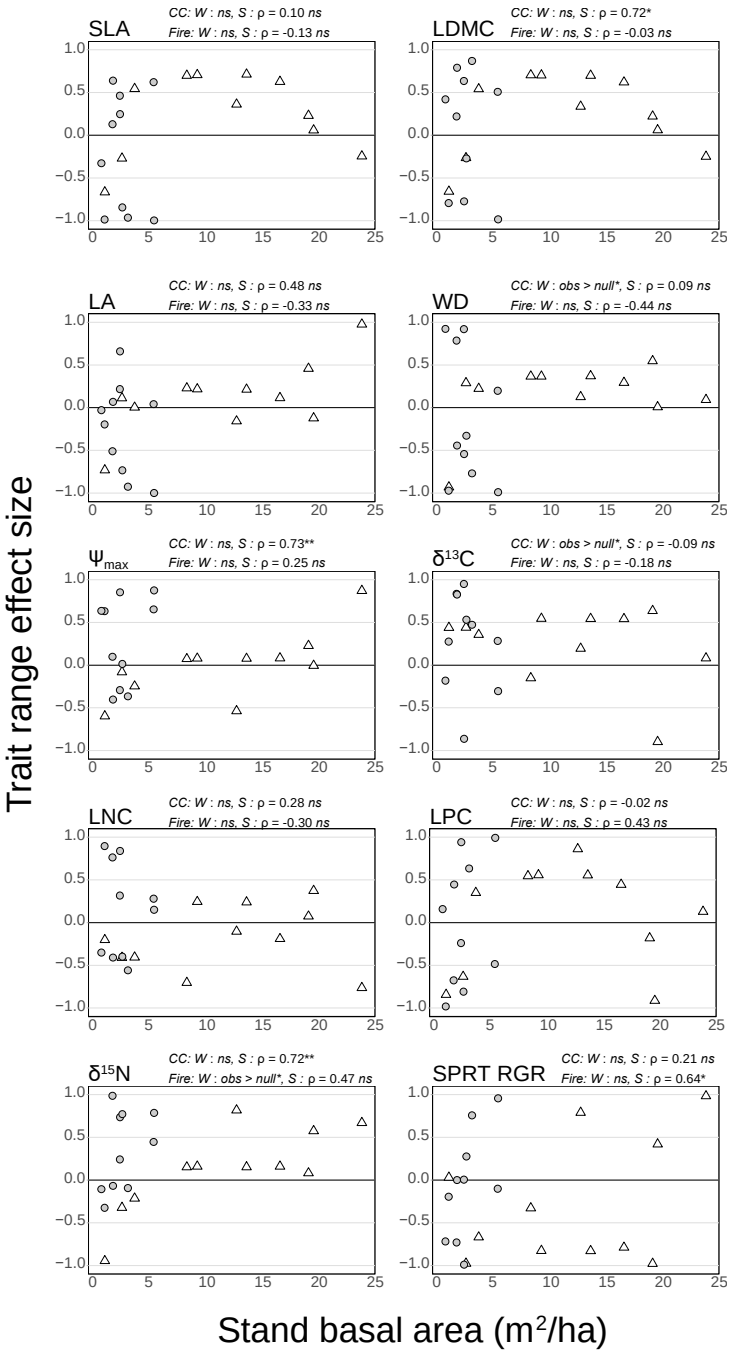


Figure D.2. Trait dispersion along the successional gradient in clearcut (open triangles) and fire (shaded circles) communities (weighted by basal area). Plots show community trait range variation relative to a null model of random assembly. Negative effect sizes are evidence of trait range reduction. Two-sided Wilcoxon tests (*W*) and Spearman's rank correlations (*S*) are labelled above panels. Abbreviations are: specific leaf area, SLA; leaf dry matter content, LDMC; leaf area, LA; wood density, WD; maximum dry season leaf water potential, ψ_{max}; carbon isotope composition, $\delta_{13}C$; leaf nitrogen content, LNC; leaf phosphorus content, LPC; nitrogen isotope composition, $\delta_{15}N$; resprout relative growth rate, SPRT RGR.

APPENDIX E

Absolute trait ranges and raw output from community assembly null models.

Table E.1. Trait ranges within clearcut and fire communities as used in our null model analysis (weighted by abundance). Abbreviations include: Community ID (com) as found in Appendix C.1. and C.2.; total species from community used in null model analysis, α; observed trait range from field data, obs range; mean null range from null distribution output, mean null range.

		Disturbance				Disturbance			
		Clearcut				Fire			
Trait	Com	α	(min-max)	obs range	mean null range	α	(min-max)	obs range	mean null range
SLA	1	12	(54 - 134.3)	80.3	83.72	11	(63.5 - 147.2)	56.7	84.63
$cm^2\ g^{-1}$	2	11	(63.5 - 147.2)	83.7	81.77	9	(63.5 - 120.2)	89.4	79.56
	3	10	(54 - 147.2)	93.2	79.66	10	(57.8 - 147.2)	53.7	82.37
	4	11	(54 - 147.2)	93.2	81.65	7	(84 - 113.3)	45.8	72.73
	5	11	(54 - 147.2)	93.2	81.8	5	(73.9 - 127.6)	63.2	62.8
	6	11	(54 - 147.2)	93.2	81.71	8	(74.4 - 120.2)	81.22	76.36
	7	11	(54 - 147.2)	93.2	81.66	9	(84 - 147.2)	83.7	79.62
	8	20	(57.8 - 151)	93.2	94.14	5	(74.4 - 155.6)	49.8	62.89
	9	8	(63.5 - 147.2)	83.7	74.46	2	(74.4 - 127.6)	53.15	30.07
	10	14	(54 - 147.2)	93.2	87.12	5	(74.4 - 147.2)	72.8	63.13
	11	16	(58.3 - 147.2)	88.9	90.23	-	-	-	-
LDMC	1	12	(0.35 - 0.53)	0.18	0.21	11	(0.28 - 0.47)	0.18	0.21
$g\ g^{-1}$	2	11	(0.28 - 0.53)	0.25	0.2	9	(0.35 - 0.53)	0.26	0.19
	3	10	(0.28 - 0.53)	0.25	0.19	10	(0.28 - 0.54)	0.19	0.2
	4	11	(0.28 - 0.53)	0.25	0.2	7	(0.34 - 0.47)	0.3	0.17
	5	11	(0.28 - 0.53)	0.25	0.2	5	(0.34 - 0.53)	0.2	0.14
	6	11	(0.28 - 0.53)	0.25	0.2	8	(0.23 - 0.53)	0.25	0.18
	7	11	(0.28 - 0.53)	0.25	0.2	9	(0.28 - 0.48)	0.19	0.19
	8	20	(0.23 - 0.55)	0.32	0.25	5	(0.23 - 0.48)	0.13	0.14
	9	8	(0.28 - 0.53)	0.25	0.17	2	(0.23 - 0.39)	0.16	0.06
	10	14	(0.28 - 0.53)	0.25	0.22	5	(0.23 - 0.47)	0.24	0.14
	11	16	(0.28 - 0.55)	0.27	0.23	-	-	-	-
LA	1	12	(3.2 - 33.1)	29.91	69.17	11	(3.2 - 100)	29.91	96.55
cm^2	2	11	(3.2 - 99.7)	96.47	64.73	9	(3.2 - 33.1)	96.32	95.79
	3	10	(3.2 - 99.7)	96.47	59.6	10	(3.4 - 99.7)	95.73	96.32
	4	11	(3.2 - 99.7)	96.47	64.76	7	(4.2 - 33.1)	61.33	92.93
	5	11	(3.2 - 99.7)	96.47	65.17	5	(4.2 - 100)	89.66	84.39
	6	11	(3.2 - 99.7)	96.47	65.27	8	(3.4 - 64.7)	94.48	94.79
	7	11	(3.2 - 99.7)	96.47	63.91	9	(10 - 99.7)	96.75	95.89
	8	20	(3.4 - 100)	96.6	94.54	5	(5.2 - 99.7)	29.91	84.27
	9	8	(3.2 - 99.7)	96.47	49.71	2	(64.7 - 100)	35.27	42.91
	10	14	(3.2 - 99.7)	96.32	78.04	5	(5.2 - 99.7)	74.64	84.69
	11	16	(1.6 - 100)	98.4	85.6	-	-	-	-
LNC	1	11	(0.86 - 2.09)	1.23	1.36	11	(0.89 - 2.16)	1.23	1.13
%	2	10	(0.89 - 2.09)	1.2	1.31	9	(0.86 - 2.09)	1.17	1.05
	3	9	(0.86 - 2.09)	0.9	1.26	8	(1.07 - 2.24)	1.28	1.02
	4	9	(0.86 - 1.76)	0.9	1.25	7	(1.66 - 2.09)	0.85	0.97
	5	9	(0.86 - 2.09)	1.23	1.26	5	(0.89 - 2.16)	0.72	0.86
	6	9	(0.86 - 2.09)	1.23	1.25	8	(1.24 - 2.09)	1.27	1.02
	7	10	(0.86 - 2.09)	1.23	1.31	9	(1.29 - 2.01)	1.28	1.06
	8	19	(0.95 - 2.93)	1.97	1.65	4	(1 - 2.17)	0.75	0.76
	9	8	(0.89 - 2.09)	1.2	1.19	2	(2 - 2.16)	0.16	0.42
	10	12	(0.86 - 2.17)	1.32	1.4	5	(1 - 2)	0.68	0.86
	11	16	(0.86 - 2.17)	1.31	1.54	-	-	-	-
LPC	1	12	(7.7 - 26.8)	19.16	21.07	11	(12.8 - 35.9)	24.71	20.65
$mmol\ kg^{-1}$	2	11	(12.8 - 32.2)	19.42	20.17	9	(11.2 - 35.9)	17.62	19.08
	3	10	(7.7 - 32.2)	24.57	19.29	10	(14.6 - 32.2)	13.96	19.98
	4	11	(7.7 - 32.2)	24.57	20.19	7	(19.1 - 26.8)	20.79	16.93
	5	11	(7.7 - 32.2)	24.57	20.12	5	(12.8 - 26.8)	15.5	13.81
	6	11	(7.7 - 32.2)	24.57	20.29	8	(12.8 - 33.6)	15.11	18.1
	7	11	(7.7 - 32.2)	24.57	20.28	9	(16.7 - 32.2)	23.1	19.16
	8	20	(14.6 - 35.2)	23.06	26.52	5	(20.1 - 35.2)	14.01	13.92
	9	8	(12.8 - 32.2)	19.42	17.16	2	(23.6 - 33.6)	10.08	6.32
	10	14	(7.7 - 35.2)	28.25	22.71	5	(20.1 - 33.6)	12.67	13.84
	11	16	(11.2 - 35.2)	24.72	24.28	-	-	-	-
ψ_{max}	1	10	(11 - 57.7)	46.7	39.83	11	(6.4 - 57.7)	60.1	47.98
-MPa	2	9	(6.4 - 57.7)	51.3	37.33	9	(11 - 71.1)	49.9	45.75
	3	9	(6.4 - 57.7)	51.3	37.41	8	(6.4 - 56.3)	48.3	44.22
	4	9	(6.4 - 57.7)	51.3	37.49	7	(11 - 48.1)	41.8	42.47
	5	9	(6.4 - 57.7)	51.3	37.51	5	(11 - 59.3)	44.7	37.38
	6	9	(6.4 - 57.7)	51.3	37.13	6	(14.5 - 56.3)	43.8	40.27
	7	9	(6.4 - 57.7)	51.3	37.37	9	(6.4 - 51.1)	51.3	45.7
	8	15	(6.4 - 60.8)	54.4	52.05	4	(6.4 - 50.2)	37.1	33.67
	9	8	(6.4 - 57.7)	51.3	35.11	2	(14.5 - 26.4)	11.9	18.85
	10	12	(6.4 - 57.7)	51.3	44.62	5	(6.4 - 44.6)	38.2	37.48
	11	15	(6.4 - 71.1)	64.7	52.14	-	-	-	-

TABLE E.1 *continued*. Trait ranges within clearcut and fire communities as used in our null model analysis (weighted by abundance). Abbreviations include: Community ID (com) as found in Appendix C.1. and C.2.; total species from community used in null model analysis, α; observed trait range from field data, obs range; mean null range from null distribution output, mean null range.

		Disturbance				Disturbance			
		Clearcut				Fire			
Trait	Com	α	(min-max)	obs range	mean null range	α	(min-max)	obs range	mean null range
$\delta_{13}C$	1	10	(29.3 -25.2)	4.04	3.23	11	(28.7 -26.1)	3.48	3.72
-‰	2	9	(29.3 -25.2)	4.04	3.05	8	(28.7 -25.2)	3.4	3.26
	3	9	(29.3 -25.2)	3.12	3.05	8	(28.6 -25.2)	3.4	3.26
	4	9	(29.3 -26.1)	3.12	3.05	7	(27.8 -25.2)	3.4	3.09
	5	9	(29.3 -25.2)	4.04	3.05	5	(28.6 -25.2)	2.36	2.65
	6	9	(29.3 -25.2)	4.04	3.04	6	(28.6 -25.2)	4.02	2.89
	7	9	(29.3 -25.2)	4.04	3.04	9	(29.3 -26.9)	2.56	3.43
	8	15	(29.3 -25.2)	4.02	3.89	4	(29.3 -25.2)	2.98	2.36
	9	8	(29.3 -25.2)	4.04	2.84	2	(27.9 -25.2)	2.68	1.32
	10	12	(29.3 -25.2)	4.04	3.55	5	(29.3 -25.2)	4.02	2.66
	11	15	(29.3 -25.2)	4.04	3.89	-	-	-	-
$\delta_{15}N$	1	10	(-1.2 - 3.8)	5	6.87	11	(-1.2 - 5.8)	7.12	6.88
‰	2	9	(-0.8 - 5.9)	6.74	6.64	9	(-1.2 - 5.9)	6.84	6.57
	3	9	(-1.2 - 5.9)	7.06	6.63	8	(-1 - 5.8)	6.44	6.35
	4	9	(-1.2 - 5.9)	7.06	6.64	7	(-0.2 - 5.8)	6.44	6.14
	5	9	(-1.2 - 5.9)	7.06	6.64	5	(-0.6 - 5.8)	5.56	5.48
	6	9	(-1.2 - 5.9)	7.06	6.62	6	(-0.6 - 5.8)	7.4	5.83
	7	9	(-1.2 - 5.9)	7.06	6.63	9	(-0.8 - 4.7)	7.06	6.57
	8	15	(-1.2 - 6.6)	7.78	7.45	4	(-0.8 - 6.6)	6.08	5.01
	9	8	(-0.8 - 5.9)	6.74	6.38	2	(1.1 - 3.6)	2.48	2.91
	10	12	(-1.2 - 6.6)	7.78	7.17	5	(-0.8 - 4.7)	5.56	5.49
	11	15	(-1.2 - 6.6)	7.78	7.47	-	-	-	-
WD	1	12	(0.73 - 1.17)	0.44	0.62	11	(0.25 - 0.96)	0.41	0.73
g cm^{-3}	2	11	(0.25 - 1.17)	0.92	0.59	9	(0.62 - 1.03)	0.78	0.63
	3	10	(0.25 - 1.17)	0.92	0.56	10	(0.25 - 1.03)	0.41	0.68
	4	11	(0.25 - 1.17)	0.92	0.59	7	(0.68 - 1.03)	0.43	0.53
	5	11	(0.25 - 1.17)	0.92	0.59	5	(0.62 - 1.03)	0.92	0.42
	6	11	(0.25 - 1.17)	0.92	0.6	8	(0.6 - 1.03)	0.92	0.58
	7	11	(0.25 - 1.17)	0.92	0.59	9	(0.25 - 1.17)	0.71	0.63
	8	20	(0.25 - 1.17)	0.92	0.83	5	(0.25 - 1.17)	0.35	0.42
	9	8	(0.25 - 1.17)	0.92	0.49	2	(0.6 - 0.72)	0.12	0.19
	10	14	(0.25 - 1.17)	0.92	0.69	5	(0.25 - 1.17)	0.92	0.42
	11	16	(0.25 - 1.17)	0.92	0.74	-	-	-	-
SPRT RGR	1	12	(18 - 132)	125.62	120.6	11	(15 - 191)	171.82	130.62
cm yr^{-1}	2	11	(20 - 160)	71.76	114.75	8	(5 - 191)	128.36	126.21
	3	10	(18 - 160)	97.75	108.36	10	(15 - 191)	149.51	129.55
	4	11	(18 - 160)	97.75	114.73	6	(18 - 191)	153.86	119.2
	5	11	(18 - 160)	78.23	114.54	4	(18 - 191)	67.16	103.96
	6	11	(18 - 160)	78.23	114.58	4	(23 - 176)	67.16	104.09
	7	11	(18 - 160)	78.23	114.7	9	(15 - 23)	107.39	128.06
	8	11	(17 - 160)	130.9	114.78	5	(15 - 28)	118.27	113.02
	9	8	(43 - 160)	57.46	95.07	1	(148)	0	0
	10	12	(18 - 160)	156.86	120.37	4	(15 - 191)	86.73	103.7
	11	12	(14 - 160)	171.82	120.58	-	-	-	-